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Late Holocene drought, fire, and vegetation in northeastern North America inferred from peatland archives

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ABSTRACT

Recent and projected increases in global temperatures, associated changes in regional moisture balance, and changes in the frequency of extreme climatic events, have raised concerns about the potential for rapid ecosystem changes. The paleoecological record is rich with examples of ecological change, and provides a long-term perspective that includes evidence of climatic extremes and ecological dynamics that exceed historical variability of the past few centuries. Although paleoecology has often focused on millennial-scale changes, examining records of past climate and ecological dynamics at high-resolution, particularly across time periods of rapid ecosystem or climatic changes may provide critical insights into ecosystem responses to climate change at timescales relevant to management and adaptation efforts. In this dissertation, I developed high resolution records of hydrological, fire, and vegetation history from peatlands in Maine, to 1) examine the linkages between hydroclimate and fire occurrence in the humid Northeast, 2) understand the drivers and spatiotemporal dynamics of an abrupt forest compositional change that occurred 500 and 600 years ago, and 3) use site-based records collectively to infer the timing of widespread climate extremes over the past 3000 years. Results indicated that drought intervals significantly increased the probability of regional wildfires, indicating strong climatic control of fire in this humid region. The most severe and widespread drought of the past 3000 years occurred between 500 and 600 yr BP, when all three studied peatlands recorded both drought and fire. A synthesis of forest pollen data from this time period showed eastern hemlock (*Tsuga canadensis*) and American beech (*Fagus grandifolia*) both rapidly declined in much of the Northeast,

while more drought tolerant pines (*Pinus* spp.) and oaks (*Quercus* spp.) increased and persisted in higher abundance until European settlement. Coupled analysis of pollen, fire, and paleohydrology from the same peat cores clearly demonstrated that this vegetation shift was in response to the drought and associated fires. A comparison of extreme dry periods and wet periods developed from three peatland records indicated that dry periods were synchronous across multiple sites, however only 67% of wet periods were synchronous among multiple sites. The most severe and prolonged dry periods were centered at 550 Cal yr BP, 800 Cal yr BP, and 2300 Cal yr BP and the time period from 400 to 1000 Cal yr BP contained the most extreme events (i.e., dry or wet phases). While ecologically significant droughts and widespread fire have not been common in the northeastern USA during the past century, this research clearly highlights the potential vulnerability of the region to future drought and fire impacts. Results also demonstrate the utility of coupled records of fire and climate in understanding regional fire-vegetation-climate dynamics, and demonstrate the usefulness of combining multiple hydroclimate records to assess regional climate and ecological history.

Introduction

This dissertation focuses on late Holocene hydroclimate variability in northeastern North America and its impact on the ecology and fire dynamics of the region. Global temperatures are expected to continue to increase over the coming century (Collins et al. 2013), while interannual and perhaps decadal variability may increase as temperatures rise (Hayhoe et al. 2007), with important potential implications for ongoing and future management of natural resources. In the past decade or two, extensive climate-induced forest mortality has occurred globally and is projected to continue as climate warms and becomes more extreme (van Mantgem et al. 2009; Allen et al. 2010). Semi-arid regions, such as the western US provides a good example for contemporary climate-induced vegetation change, where drought and fire have altered vegetation in many parts of the region (i.e., Breshears et al. 2005). However in humid regions such as the densely populated Northeast, ecologically significant droughts and fires have been relatively infrequent during the past 100 years, however, some evidence suggests that the region has recently been unusually wet during this century (Pederson et al. 2013). Records of moisture variability and extreme events from the past millennia or longer are needed to provide a more complete description of climate variability in the Northeast, as well as examples of climate-induced ecosystem changes that can be studied at high resolution to gain insight into drivers and ecological dynamics that are not observable in datasets from the past century.

The hydroclimate from three raised bogs located in Maine was reconstructed using testate amoebae as indicators of water-table depth and peat humification as another

proxy of hydroclimate. I coupled these records with pollen and charcoal analyses to examine the dynamics of hydroclimate, fire, and vegetation, with a focus on times of abrupt changes. The first and second chapters of this dissertation focus on the role of, multidecadal drought in affecting the probability of fire at local and regional spatial scales, and the role of drought and fire in driving widespread and rapid changes in forest community composition. Chapter 1 examines the relationships between climatic state (i.e., dry and wet periods) and the probability of fire occurrence. Chapter 2 describes how drought and fire drove a rapid vegetation shift at 500 to 600 Cal yr BP. The rapid vegetation shift at 500 to 600 Cal yr BP has been described in many studies, but a driver for this vegetation change has been unclear. Chapter 3 examines methods of compiling and stacking the three peatland hydroclimate records using water-table depth, peat humification and charcoal records collectively to provide assessment of the reconstructions.

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Chapter 1: Increased probability of fire during late Holocene droughts in northern New England

Abstract

Understanding the role of fire in the Earth system, and particularly regional controls on its frequency and severity, is critical to risk assessment. Charcoal records from lake sediment and fire-scar networks from long-lived tree species have improved our understanding of long-term relationships between fire events and climate. This work has primarily focused on historically fire-prone ecosystems and regions. In the northeastern USA, where wildfire has been relatively infrequent in historical times, fire-risk assessments have incorporated little-to-no pre-historical data and little is known about long-term fire-climate relationships. We developed coupled, high-resolution records of moisture variability and fire from three ombrotrophic peatlands in Maine using testate amoebae and analysis of microscopic charcoal. Water-table depth reconstructions among the three sites were generally coherent, with high-magnitude dry and wet events corresponding within the uncertainty of age-depth models. At all sites, there was a significantly higher probability of fire events during high-magnitude droughts. However, although prolonged droughts were widespread and associated with higher probability of fire, the fire events were rarely synchronous among sites, with the exception of ~550 years before present (yr BP) when all three sites experienced both drought and fire. While fire has been relatively uncommon in the northeastern USA during the past century, our records clearly highlight the potential vulnerability of the region to future drought and

fire impacts. Results also demonstrate the utility of coupled records of fire and climate in understanding regional fire-climate dynamics.

Introduction

Increasing frequency of extreme climatic events, such as heat waves and drought, is an expected consequence of global climate change (Easterling et al. 2000; Meehl and Tebaldi 2004; Hansen et al. 2012), and understanding the ecological effects of such events is critical to risk assessment. For example, heat waves and drought can alter fire dynamics in forested ecosystems, leading to increased fire-season length, fire size, and burn severity (Gillett et al. 2004; Westerling et al. 2006). Furthermore, extreme events may increase the extent or frequency of disturbances such as insect outbreaks, blowdowns, and ice storms, all of which alter forest fuel composition and fire dynamics (e.g., Dale et al. 2001). Model projections of future climate suggest that many regions of North America will dry in the coming century (Solomon et al. 2009; Overpeck and Udall 2010), further increasing the probability of ignitions (Westerling et al. 2006; Moritz et al. 2012). However, even regions not projected to undergo long-term drying are expected to experience increased extreme events as global temperatures continue to warm (Easterling et al. 2000; Hansen et al. 2012), which may lead to higher probabilities of fire occurrence (Westerling et al. 2006; Moritz et al. 2012).

Historical records of climate and fire occurrence for the past several decades-to-century have provided valuable insights into the relationship between climate and fire in a range of North American ecosystems (e.g., Westerling et al. 2006; Littell et al. 2009).

Such studies have linked weather, climate regimes, and ocean-atmospheric teleconnections to historical fire occurrences and burn dynamics in different vegetation and fuel systems, and have increased prediction power of near-term fire danger (e.g., Bradshaw et al. 1984; Westerling et al. 2003; Priesler and Westerling 2007). However, studies spanning the past century may not capture the natural range of variability in fire frequency and extent, and may incompletely describe fire-climate relationships. Given anticipated changes in global climate, long-term perspectives on regional fire-climate relationships are needed.

Charcoal records from lake sediment and fire-scar networks derived from long-lived tree species have provided long-term perspectives on fire regimes (e.g., Swetnam and Betancourt 1990), and when coupled with paleoclimate records have improved our understanding of the sensitivity of fire events to climate change (e.g., Colombaroli and Gavin 2010). For example, climate variability is clearly an important control on fire frequency and extent in semi-arid western North America (Swetnam and Betancourt 1990; Kitzberger et al. 2007; Trouet et al. 2010). Higher productivity during wet periods increases fuel loadings, which may then burn during droughts (Roos and Swetnam 2012). While land-use practices of the past several centuries have altered vegetation and fire dynamics (e.g., Fuller et al. 1998; Swetnam et al. 1999), climate still exerts a strong control on fire in many regions (Littell et al. 2009; Krawchuk and Moritz 2011).

In the densely populated northeastern USA, where wildfire has been relatively infrequent historically, long-term relationships between moisture variability and fire have not been adequately assessed and fire-risk assessments for this region have incorporated

little-to-no pre-historical data (e.g., United States Forest Service 2010). Tree-ring based hydroclimate reconstructions suggest that recent decades in the region have been unusually wet (Pederson et al. 2013), yet climate models suggest that future temperatures in the northeastern USA will continue to increase, as will the frequency of summer drought events (Anderson et al. 2010). Recent assessments of climate change impacts on forests of the region have noted the potential for increased fire frequencies in the future (e.g., Frumhoff et al. 2007; Maine Forest Service 2010); however, long-term data from the region supporting these predictions are lacking, and much local variability will likely exist due to differences in forest types and fuel characteristics (United States Forest Service 2010). Although sediment-based fire reconstructions exist in eastern North America (e.g., Clark et al. 1996; Parshall and Foster 2002; Hotchkiss et al. 2007), few of these records have sufficient chronological control to allow direct comparison of hydroclimate and fire events (e.g., Tweiten et al. 2009; Shuman et al. 2009).

In this paper, we developed records of water-table depth and charcoal influx from three peatlands in Maine to assess patterns of multidecadal drought and fire for the past 3000 years. We used testate amoebae to reconstruct water-table depth changes and microscopic charcoal to reconstruct fire events. Contiguous analyses of both hydroclimate and fire from within the same sediment cores allowed direct comparison of these records, independent of any chronological uncertainty. We also assessed long-term fire-climate relationships at these sites in a probabilistic fashion, and used our data to discuss potential future risk of drought and fire in this humid region.

Methods

Sediment cores were collected with a wide-diameter piston corer from three ombrotrophic peatlands in Maine (Figure 1.1). All peatlands were dominated by *Sphagnum* and ericaceous shrubs, with widely scattered trees. Regional upland forests around Saco Bog were dominated by pines (*Pinus* spp.) and oaks (*Quercus* spp.) whereas regional vegetation surrounding the other two sites consisted of mesic-hardwood and mixed-hardwood forest. Peat cores were returned to the laboratory and sliced into contiguous 1-cm intervals, and 1-cm^3 subsamples were collected for analysis of testate amoebae and microscopic charcoal. Both proxies were examined in every centimeter along cores from the three sites. A known number of *Lycopodium* marker grains were added so that concentrations could be calculated. Testate amoeba processing and taxonomy followed standard methods (e.g., Booth et al. 2010), where samples were sieved and the fraction between 15 µm and 300 µm was retained for analyses. For testate amoeba analysis, microscope slides were generally scanned until a total of at least 100 testate amoebae were identified and counted; however, in a few samples preservation was poor and densities were low so only 50 individuals were counted, which is typically still adequate for transfer function applications (Payne and Mitchell 2009).

Standard methods were used to establish chronologies along the cores and age-depth models were created using a flexible Bayesian modeling framework in the program Bacon (Blaauw and Christen 2011). We collected 15 radiocarbon dates from Sidney Bog, 22 from Great Heath (Nichols and Huang 2012), and 15 from Saco Bog (Table 1.1). At each site, the rise in *Ambrosia* spp. pollen indicating European land-clearance was set to

150 years before present (yr BP), where present was defined as 1950 AD. The mean accumulation rate was determined by linear regression analysis of the calibrated radiocarbon dates and used to define the *a priori* distribution of the accumulation rate for the age-depth model.

We counted all charcoal fragments on the slides prepared for testate amoeba analysis, so our charcoal data includes all fragments between 15 µm and 300 µm in diameter. Microscopic charcoal counts have been shown to correspond to regional fire signals in lake sediments (Clark and Royall 1995; Tinner and Hu 2003), and are suitable for examining fire-climate relationships (e.g., Tinner et al. 1998; Carcaillet et al. 2001a). Although peatland records of microscopic charcoal have not been as extensively calibrated as those of lakes, good correspondence in records from the same peatland and nearby lake records have been observed (Innes et al. 2004; Rius et al. 2011), and at least for ombrotrophic peatlands, most microscopic charcoal is deposited directly from the atmosphere, and not through other sedimentation processes. However, it is possible for peatland vegetation and the peat itself to burn, producing abundant charcoal and charred peatland-plant remains, and potentially resulting in a depositional hiatus.

Analytical methods for charcoal and testate amoeba-based moisture reconstructions followed standard protocols. For water-table depth reconstructions, a weighted-average model developed from a calibration dataset of 650 modern samples in North America was used (Booth 2008). Reconstructed water-table depths were then detrended to remove millennial-scale variability in the record, which may be unrelated to climate and caused by autogenic factors, such as lateral bog growth (Charman et al.

2006). Detrending was performed using a LOESS curve applied to 1000 years (Figure 1.2). Charcoal counts were transformed to influx, or charcoal accumulation rates (CHAR). CHAR was treated in a similar manner as in Power et al. (2008), where CHAR data were min-max transformed to standardize the scale among sites, and then Box-Cox transformed to normalize the highly skewed CHAR data, and subsequently standardized using z-scores which were used to identify fire events.

Relationships between moisture variability and CHAR peaks were compared visually within each site, as well as probabilistically. To determine the probability that a fire occurred during certain climate state (i.e., drought, average, or pluvial), water-table depth extremes (25^{th} and 75^{th} percentiles) were used to classify samples as drought and pluvial climate states, respectively. We used a CHAR threshold of 1 standard deviation to identify fire events. We then calculated the probability of fire events during drought, average, and pluvial climate states as determined by our CHAR and drought thresholds. A χ^2 test was used to determine if fire events at each site occurred at significantly different probabilities among the different climate states. Each site was analyzed individually in a 1×3 contingency table, where observed values were calculated as the probability of fire occurrence within each climate state. Expected values were calculated as the probability of fire occurring at any time within each record (i.e., samples with fire/total samples). We also performed a sensitivity analysis to determine whether our thresholds for climate states and drought events altered our interpretation of fire probabilities. Data from the time period 200 yr BP to the present was not used in

probability analyses or z-score calculations so that European settlement and land-clearance did not confound the fire-climate comparisons.

Results and Discussion

Age-depth models show average accumulation rates varied among the sites (Figure 1.S1), but were within the typical range for peatlands in eastern North America (Goring et al. 2012). Sidney Bog and Great Heath have accumulated peat continually during the time period analyzed; however at Saco Bog a large visible charcoal band occurs in the peat profile and the time period between ~1500 yr BP and ~580 yr BP was missing (Figure 1.2 and Figure 1.S1), indicating that the peatland burned and fire likely consumed peat. Charred *Sphagnum* remains were also recovered from this interval. Testate amoeba community composition was variable in the cores, and species that are good indicators for moisture conditions were abundant in all three records (Figure 1.S2, 1.S3, and 1.S4).

Multiple lines of evidence have demonstrated the climatic sensitivity of testate amoeba records from ombrotrophic peatlands (e.g., Charman 2007; Booth 2010; Amesbury et al. 2012), and like other paleoclimate archives, replication of patterns at multiple sites within the same climatic region can be used to identify and validate climate signals. Although autogenic factors can influence surface-moisture records obtained from peatlands (e.g., Charman et al. 2006; Swindles et al. 2012), we focus our interpretation on the large, extreme events, and these are generally coherent among our sites, at least within the uncertainty of the age-depth models (Figure 1.3). Smaller-magnitude

fluctuations, long-term (i.e., millennial-scale) variability, or patterns not replicated among sites may result from autogenic processes. Our three records from Maine reveal that large-magnitude drought and pluvial events are captured in these records, making them well suited to exploring fire-climate linkages (Figure 1.3).

The largest peaks in CHAR occurred during times of prolonged and widespread drought, indicating strong climatic control of fire in the regions surrounding our sites in Maine (Figure 1.3). For example, at Sidney Bog all of the largest CHAR peaks correspond with droughts, and at Great Heath and Saco Bog most of the large CHAR peaks correspond with drought. The major exception is after European land-clearance in the Saco Bog record, when large peaks occur in the absence of drought. Land use changes and forest clearance likely altered fire-climate relationships at this time. Sample-by-sample probabilistic analyses support these visual observations, and indicate that the probability of fire increased significantly during drought periods relative to average or pluvial conditions at all sites (Figure 1.4, Table 1.2). For example, fire events were 8-fold, 2-fold, and 5-fold as likely during drought periods versus pluvial periods at Sidney Bog, Great Heath, and Saco Bog respectively. Choice of thresholds for the categorization of drought and fire events had little effect on our overall results and interpretation, with significantly higher probability of fire during drought episodes using a range of realistic thresholds (Figure 1.S5).

Although we interpret our charcoal records as primarily reflecting fires in the regional uplands surrounding our sites, it must be noted that local peatland fires likely produced some of the charcoal in these records; as was certainly the case during the

depositional hiatus at Saco Bog. However, if peatland vegetation fires were a dominant source of charcoal throughout our records, we would have expected larger pieces of charcoal as well as remains of charred peatland vegetation (Clark 1988; Clark et al. 1998; Carcaillet et al. 2001a). While the source area of microscopic charcoal can be extensive (e.g., Tinner et al. 2006), most studies suggest it is similar to that of wind-blown pollen (Clark 1988; Carcaillet et al. 2001a). Furthermore, examination of peat stratigraphy from our sites indicates domination by *Sphagnum* moss and ericaceous shrubs throughout the past 1000 years, and woody shrub vegetation would be expected to produce large charcoal fragments if burned. Although we did not measure charcoal fragments in this study, based on routine comparison with the testate amoebae and pollen in the samples, the majority of the charcoal fragments were well below 100 µm in size, except during the hiatus at Saco Bog, where larger charcoal fragments were associated with abundant charred *Sphagnum* leaves and stems. No other samples from any of the peat cores contained charred *Sphagnum* or abundant large charcoal fragments.

Differences in forest vegetation likely explain the differences in the absolute values of CHAR, and the differences in the strength of fire-climate relationships among sites (Figure 1.3). For example, pre-settlement vegetation near Saco Bog included higher proportions of pines and oaks than the other sites (Lorimer 1977; Cogbill et al. 2002). The pine-oak forests of New England burned more frequently than mesic-hardwood and mixed-hardwood forests, like those surrounding Sidney Bog and Great Heath (Lorimer 1977; Fahey and Reiners 1981; Fuller et al. 1998). The increased occurrence of fire in the pine-dominated region around Saco Bog likely accounts for the higher absolute and

background CHAR values, excluding the peak caused by peatland burning, while hardwood sites likely burned less frequently, although these fires were probably linked more closely to prolonged drought events (Figure 1.3, 1.4). Although the distance from the coring location to the peatland edge might also be expected to influence CHAR values, this distance was relatively similar among our sites (e.g., ~500 m).

Regional fire and vegetation records show that fires occurred in most forest types of the region during the late Holocene (e.g., Foster et al. 2002; Parshall and Foster 2002), although fires were more common when conifers were a larger component of the vegetation in the early Holocene (Talon et al. 2005). Clearly vegetation is a strong determinant of fire occurrence in the region, and more frequent fires occur in pine, chestnut (*Castanea* sp.), and oak-dominated forests than other hardwood-forest types (Fahey and Reiners 1981; Parshall et al. 2003; Talon et al. 2005). Our records are not inconsistent with the importance of forest vegetation as a control on fire occurrence; however, our records reveal that the probability of fire in both pine and hardwood-dominated forests increased during late Holocene droughts. Several studies have previously suggested that climate may have been a primary control on fire in the region during the late Holocene (Carcaillet et al. 2001b; Parshall and Foster 2002), and information from the past century indicate increased occurrence and burn area of fires during summer droughts (Fahey and Reiners 1981). Although some of the microscopic charcoal in our records may be derived from local vegetation immediately surrounding the peatland margins, the regional source area of microscopic charcoal suggests that much was derived from fires in the adjacent upland forests (Clark 1988). However, more

work is clearly needed to better calibrate the peatland charcoal record so that more quantitative interpretations are possible.

During the past 3000 years, fires in our records occurred primarily during regional drought events, although they were rarely synchronous among sites (i.e., not every site burned during the same drought event), highlighting the potential pitfalls of assessing climatic control of wildfire by comparing synchroneity of charcoal records within a region (i.e., Gavin et al. 2006). Patterns are consistent with the generally heterogeneous nature of fire, and although any particular area was more likely to burn during drought, fires were typically patchy on the landscape. Our results highlight the value of using independent records of fire and paleoclimate to assess regional fire-climate relationships, and similar efforts could be applied to better understand fire-climate dynamics in other regions and ecosystem types. While we focus on fire-climate relationships in this paper, Native American populations may have impacted vegetation composition and fire regimes in the region (e.g., Munoz et al. 2010); however, regardless of ignition source, our records suggest that fires occurred much more frequently during dry time periods.

Although our coupled fire-climate records reveal coherent temporal patterns of drought that were linked to heterogeneous spatial patterns of fire, a notable exception occurred at ~550 yr BP, when all three sites experienced both drought and fire (Figure 1.3). Interestingly, this was a time of widespread change in forest composition throughout much of New England (Fuller et al. 1998). For example, Fuller et al. (1998) showed that mesic, fire intolerant tree species like American beech (*Fagus grandifolia*) and eastern hemlock (*Tsuga canadensis*) declined from previous levels at this time, while more xeric

and fire tolerant species like pine, oak, and bracken fern (*Pteridium* spp.) increased in many locations. Patterns are consistent with widespread drought and fire. In fact, forest changes at this time were likely the largest of the past 1000 years, excluding land-clearance (e.g., Fuller et al. 1998). Future work could test the hypothesis that these forest changes resulted from the widespread drought and fires at 550 yr BP, by coupling records of fire, climate, and vegetation within the same sediment cores, as has been done to examine ecosystem responses to other climate events of the Holocene (e.g., Booth et al. 2012a, 2012b).

Climate has been an important control on the probability of fire in Maine during the late Holocene, at both hardwood and pine-dominated locations (Figure 1.3). Although fires have been relatively infrequent in New England during historical times, recent decades in New England have been anomalously wet (Pederson et al. 2013). Our long-term records, when viewed in conjunction with modeling results indicating increased potential for extreme events and variability in the ocean-atmosphere system (e.g., Yang and Zhang 2008; Hansen et al. 2012), suggest that the recent lack of fire may not be representative of the future. Although pre-European settlement forests in eastern North America burned relatively infrequently during the late Holocene, some fire events had significant ecological consequences and left persistent legacies (Foster and Zebryk 1993; Fuller et al. 1998; Booth et al. 2012a), highlighting the importance of long-term perspectives in fire-risk assessment. Although future fire risk in the region will vary locally due to vegetation type and other factors, enhanced hydroclimate variability and drought will likely increase the possibility of fire and ecological change. Furthermore,

even infrequent burning of highly productive forests can emit large amounts of carbon into the atmosphere (van der Werf et al. 2010; French et al. 2011) and alter biophysical feedbacks within the Earth system (Bowman et al. 2009), further underscoring the need to better understand fire-climate relationships in different regions and ecosystem types.

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Table 1.1. List of radiocarbon dates collected from each site.

Site	Lab Sample ID	Material Dated	Depth (cm)	^{14}C age	^{14}C error
Sidney Bog	UCIAMS-84643	*Sphagnum* stems	16	330	15
Sidney Bog	UCIAMS-84644	*Sphagnum* stems	25	695	20
Sidney Bog	UCIAMS-84645	*Sphagnum* stems	28	785	15
Sidney Bog	OS-80205	*Sphagnum* stems	30	1000	30
Sidney Bog	UCIAMS-84646	*Sphagnum* stems	34	935	15
Sidney Bog	UCIAMS-84647	*Sphagnum* stems	45	1190	15
Sidney Bog	OS-80206	*Sphagnum* stems	50	1180	25
Sidney Bog	UCIAMS-89815	*Sphagnum* stems	81	1525	15
Sidney Bog	OS-80207	*Sphagnum* stems	96	1740	25
Sidney Bog	OS-80208	*Sphagnum* stems	117	1980	30
Sidney Bog	UCIAMS-89816	*Sphagnum* stems	134	2840	20
Sidney Bog	OS-80209	*Sphagnum* stems	137	3050	35
Sidney Bog	OS-80210	*Sphagnum* stems	157	3270	25
Sidney Bog	OS-80211	*Sphagnum* stems	196	3670	25
Sidney Bog	OS-80212	*Sphagnum* stems	216	3950	30
Great Heath	OS-73922*		20.5	270	25
Great Heath	OS-73923*		30.5	235	25
Great Heath	UCIAMS-84649	*Sphagnum* stems	35.5	385	20
Great Heath	OS-69742*		40.5	415	30
Great Heath	OS-73924*		50.5	385	25
Great Heath	OS-73925*		60.5	615	30
Great Heath	UCIAMS-84640	*Sphagnum* stems	63.5	605	20
Great Heath	UCIAMS-84641	*Sphagnum* stems	67.5	630	15
Great Heath	OS-73926*		70.5	850	25
Great Heath	UCIAMS-84642	*Sphagnum* stems	75.5	840	15
Great Heath	OS-69743*		80.5	1010	30
Great Heath	OS-73927*		90.5	1040	30
Great Heath	UCIAMS-78208	*Sphagnum* stems	95.5	990	15
Great Heath	UCIAMS-78209	*Sphagnum* stems	105.5	1445	15
Great Heath	OS-69744*		109.5	1720	30
Great Heath	UCIAMS-78210	*Sphagnum* stems	120.5	1685	15
Great Heath	OS-69908*		139.5	2060	40
Great Heath	OS-69745*		159.5	2220	30
Great Heath	OS-69746*		185.5	2590	35
Great Heath	OS-69747*		217.5	3070	30
Great Heath	OS-69748*		257.5	3480	40
Great Heath	OS-69884*		287.5	3830	35

Saco Bog	UCIAMS-84648	*Sphagnum* stems	43	215	15
Saco Bog	UCIAMS-84649	*Sphagnum* stems	64	85	20
Saco Bog	UCIAMS-84650	*Sphagnum* stems	97	325	20
Saco Bog	OS-91555	*Sphagnum* stems	105	Modern - not used	
Saco Bog	OS-91557	*Sphagnum* stems	115	435	25
Saco Bog	OS-101271	Charcoal	119	540	30
Saco Bog	OS-91562	*Sphagnum* stems	128	705	30
Saco Bog	UCIAMS-89812	*Sphagnum* stems	135	1570	15
Saco Bog	UCIAMS-89813	*Sphagnum* stems	151	290	15
Saco Bog	OS-91556	*Sphagnum* stems	155	1940	35
Saco Bog	OS-91563	*Sphagnum* stems	175	2010	25
Saco Bog	UCIAMS-89814	*Sphagnum* stems	189	2075	15
Saco Bog	OS-91558	*Sphagnum* stems	236	2240	30
Saco Bog	UGAMS-10674	*Sphagnum* stems	247	2410	25
Saco Bog	UGAMS-10675	*Sphagnum* stems	260	2520	25

*Data from Nichols and Huang (2012).

Table 1.2. χ^2 contingency table used for each site to analyze the probability of fire occurrence during difference climate states.

Site	Drought Probability	Average Probability	Pluvial Probability	Expected Value	χ^2	df	*P*-value
Sidney Bog	25.81	14.52	3.23	14.52	17.56	2	< 0.001
Great Heath	23.53	6.06	11.76	11.94	14.15	2	< 0.001
Saco Bog	20.00	7.22	4.00	9.64	15.03	2	< 0.001

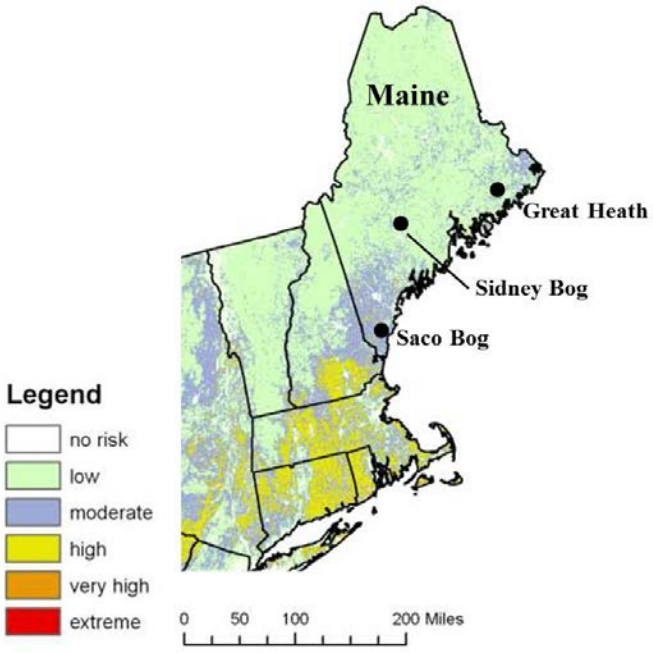

Figure 1.1. Location of study sites in northern New England overlaid on a recent wildfire risk assessment (United States Forest Service 2010)

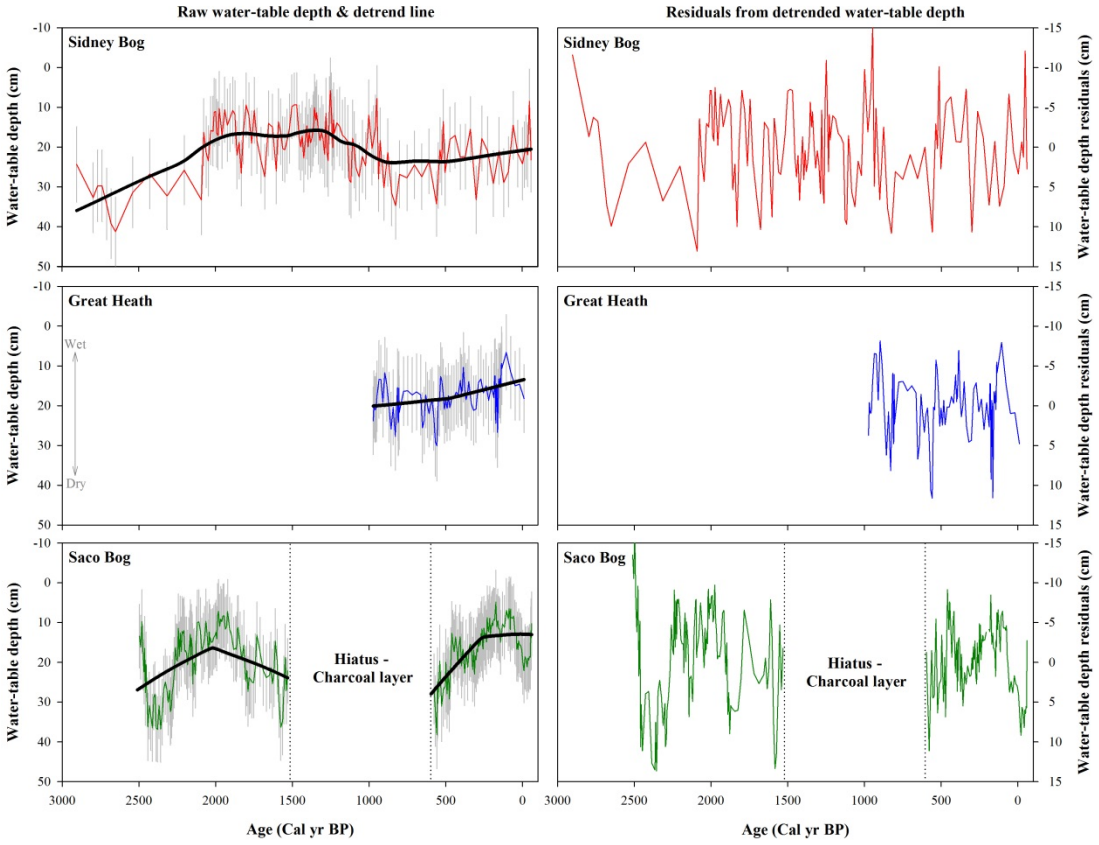

Figure 1.2. Left side panels show raw water-table depth reconstructions (colored line) and bootstrapped (n=1000) error estimates (vertical gray bars) for each site (Sidney Bog – red, top; Great Heath – blue, middle; Saco Bog – green, bottom). The black lines represent the LOESS curve used to remove millennial-scale trends in the data (1000 yr window, except for post-hiatus portion of Saco where a 650 yr window was used). Right side panels show the residuals of detrended water-table depths for each site

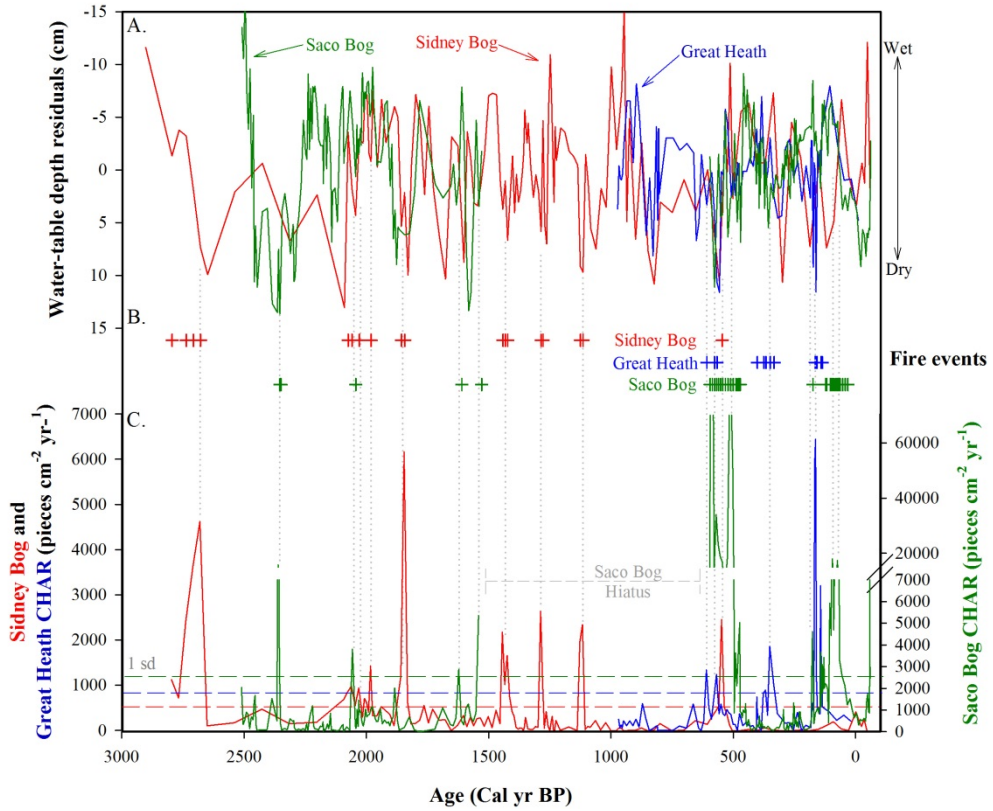

Figure 1.3. (A) Water-table depth reconstructions after detrending to remove long-term patterns show hydroclimate records from the three study sites. Most extreme hydroclimate fluctuations are coherent among sites, particularly prior to European land-clearance and associated disturbance. (B) Crosses show fire events recorded at each site (peaks above 1 standard deviation). (C) Time series of CHAR for each site. Gray dotted vertical lines highlight the visual peaks in charcoal for each site. Colored horizontal dashed line shows the 1 standard deviation threshold used to identify fire events

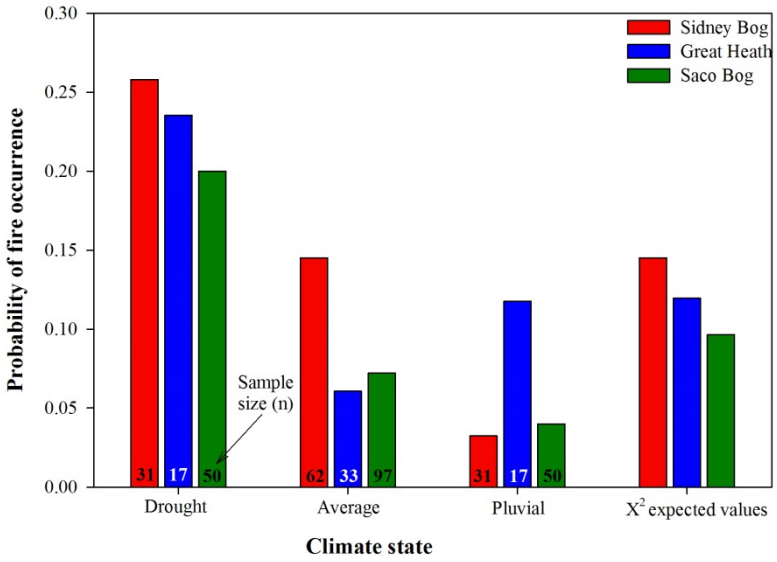

Figure 1.4. The probability of fire occurrence during drought, average, and pluvial climate states for each site. Also shown are the expected values used to compute the χ^2 test. Numbers at base of bars indicate the sample size (i.e., centimeter intervals of core) classified in each climate state. Probabilities were calculated on data prior to 200 yr BP, to remove any effect of European land-clearance on the long-term patterns

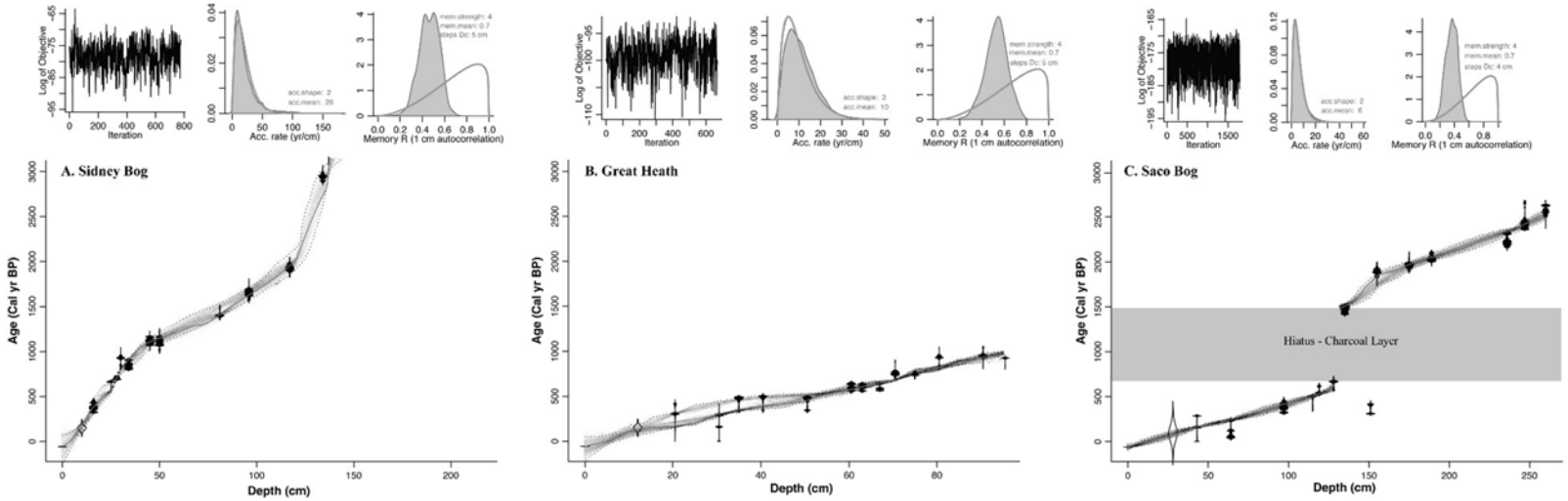

Figure 1.S.1 Age-depth models from Sidney Bog (left), Great Heath (middle), and Saco Bog (right). Top graphs are the prior distributions used to develop age-depth models (Blaauw and Christen 2011). Lower graphs show the age-depth models for each site. The black probability density dots show the probability distribution of the calibrated ^{14}C dates. The gray shaded region is a 95% envelope, with darker gray shading occurring in regions with higher probability density. Solid line represents the best fit line.

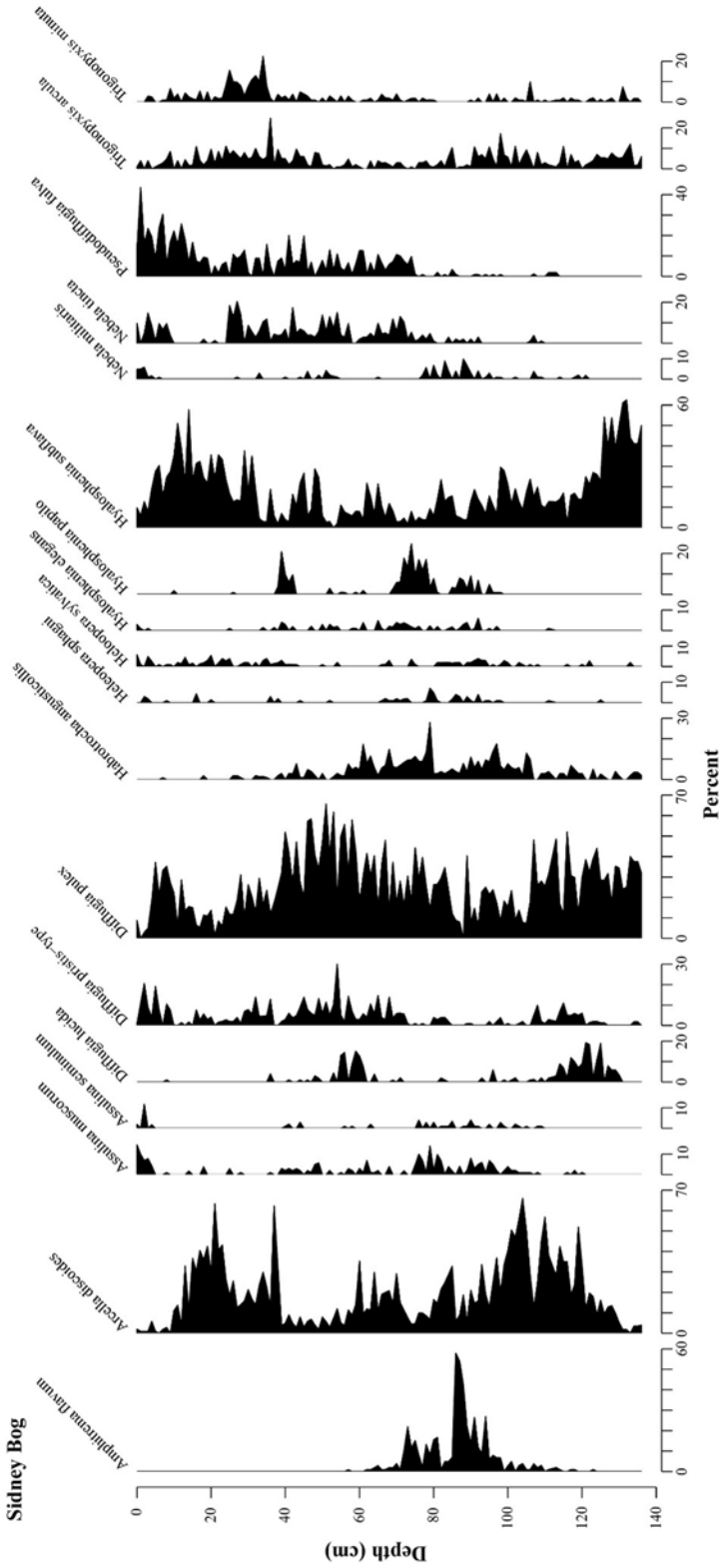

Figure 1.S2. Stratigraphic community composition of testate amoebae from Sidney Bog.

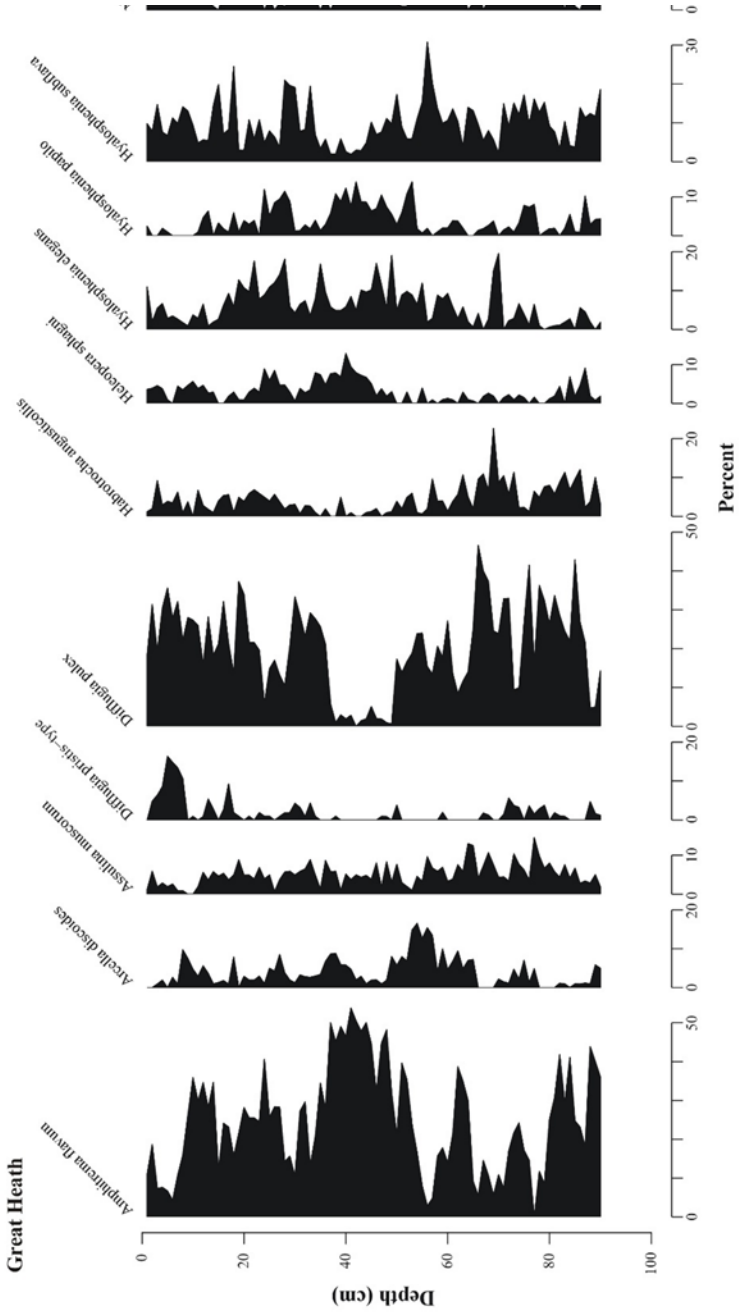

Figure 1.S3. Stratigraphic community composition of testate amoebae from Great Heath.

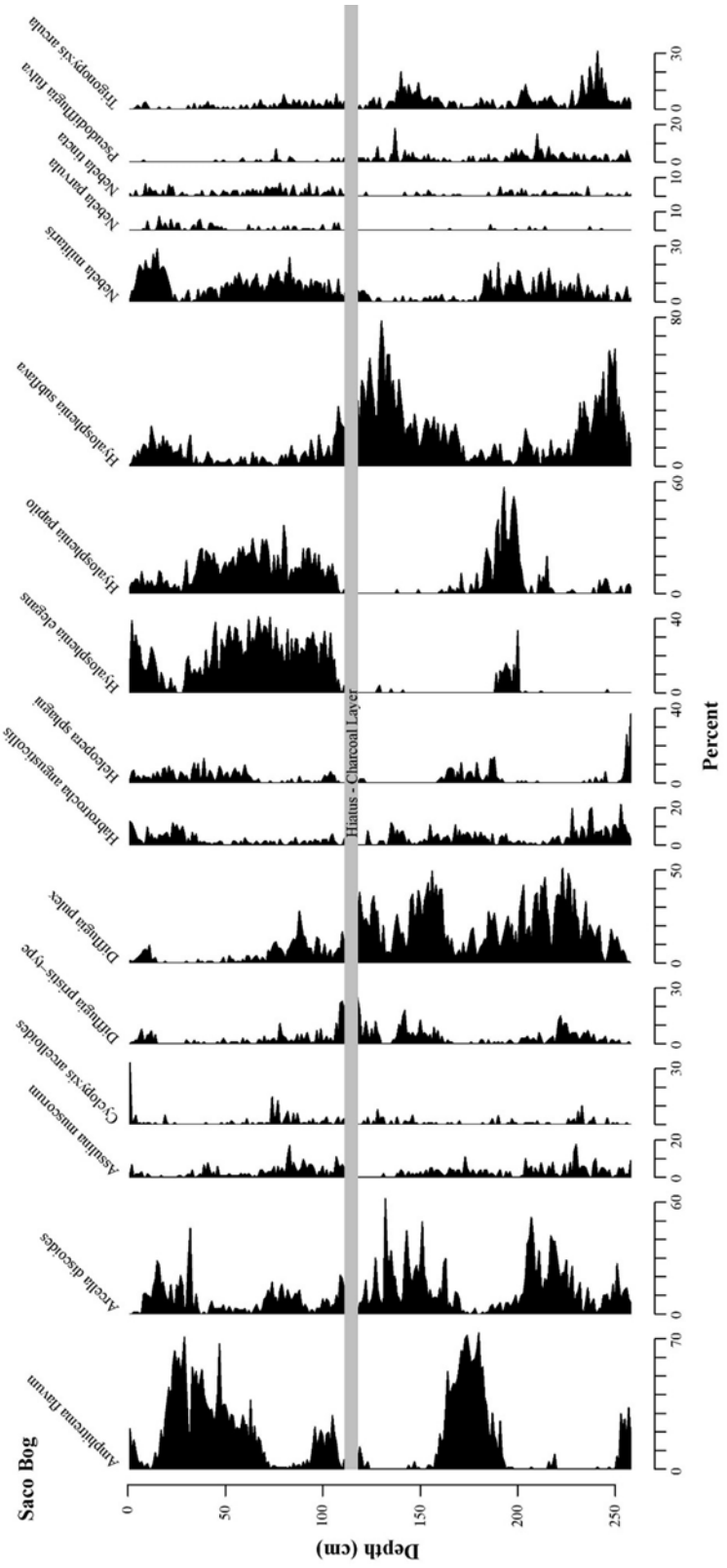

Figure 1.S4. Stratigraphic community composition of testate amoebae from Saco Bog.

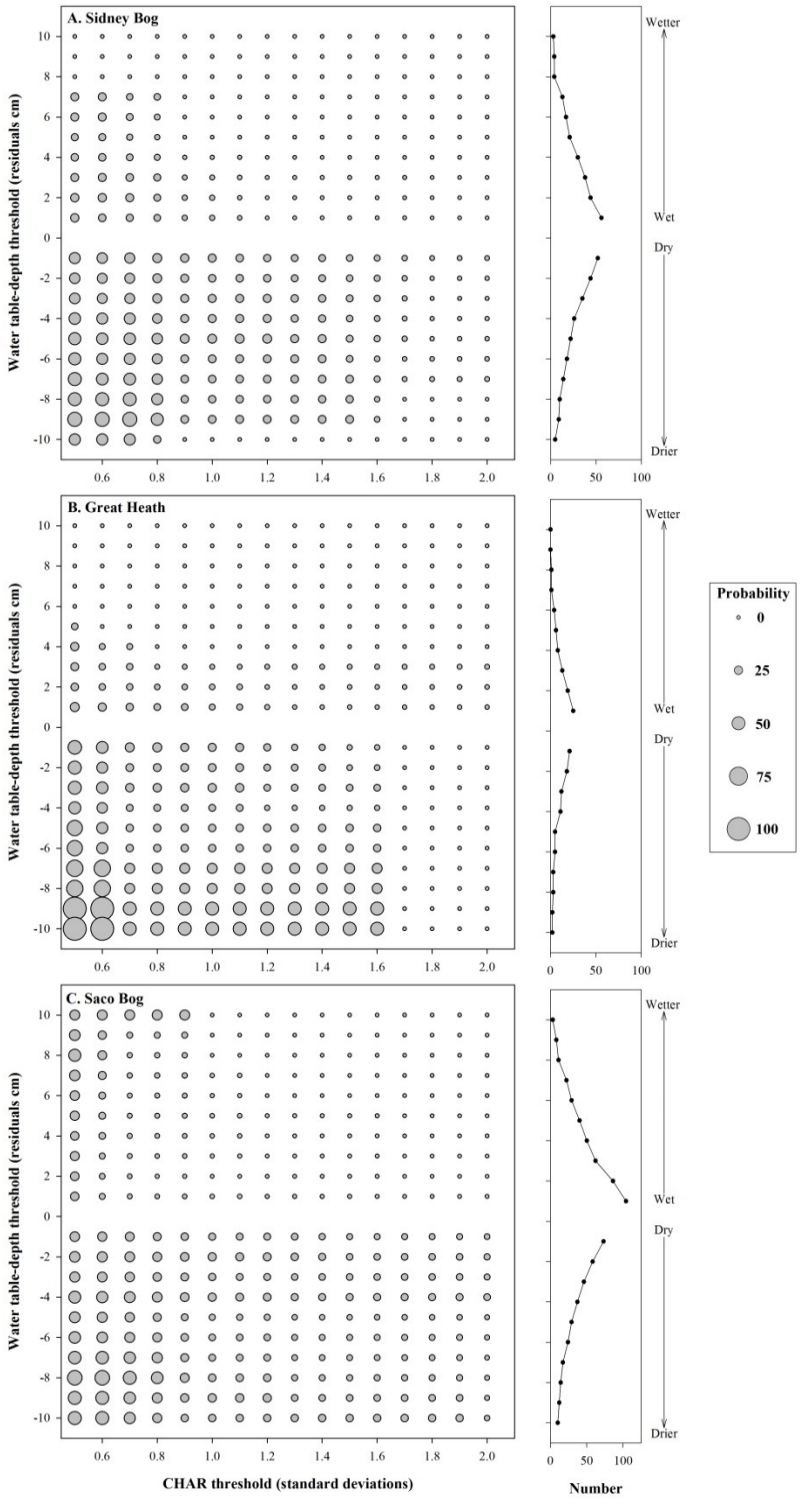
A. Sidney Bog
B. Great Heath
C. Saco Bog
Water table-depth threshold (residuals cm)
CHAR threshold (standard deviations)
Number
Wetter
Wet
Dry
Drier
Probability
0
25
50
75
100

Figure 1.S5. Threshold analyses of water table-depth residuals and CHAR standard deviations, which shows the probability of fire occurrence by incrementally increasing or decreasing values of CHAR or wetness/dryness. The graph on the right shows the number of samples for each water table-depth threshold value used in the probability calculation. Probability of fire is shown by circle size for all drought and fire threshold values that resulted in at least 1 total samples. CHAR standard deviations were calculated according to Power et al. (2008).

Chapter 2. Late-Holocene drought and fire drove a widespread change in forest community composition in eastern North America

Abstract. Several regions of the world have recently experienced climate-induced changes in forest composition, highlighting the need to understand the causes, likelihood, and dynamics of abrupt vegetation change. Although few historical examples of climate-induced forest change exist from recent centuries, particularly in humid regions like the northeastern United States, paleoecological records are rich with examples. For example, pollen records from portions of the northeastern United States indicate that eastern hemlock (*Tsuga canadensis*) and American beech (*Fagus grandifolia*) abruptly declined in abundance between 500 and 600 yr BP. Concomitant increases in pine (*Pinus* spp.) and oak (*Quercus* spp.) occurred. Hypotheses to explain this change have included cooling during the 'Little Ice Age' (LIA), Native American activity, drought, and/or fires. To better understand spatiotemporal patterns of forest change and assess potential causes and dynamics, we synthesized regional pollen records and developed two high-resolution, coupled records of vegetation, fire, and drought from bogs in Maine. Results of our synthesis reveal >70% of regional pollen sites recorded shifts in forest composition during this time period. Bog records revealed that forest composition changed a few decades after the onset of drought and regional fires, consistent with increased recruitment of pine and oak during post-disturbance succession. Vegetation changes persisted until European settlement. Our data demonstrate that widespread, long-lasting forest changes were triggered by decadal-to-multidecadal drought and associated fires,

highlighting the potential for abrupt, long-lasting forest changes in response to transient climate and disturbance events, particularly when such events occur against the backdrop of more gradual temperature change.

Introduction

Recent and projected increases in global temperatures, associated changes in regional moisture balance, and changes in the frequency of extreme climatic events, have raised concerns about potential rapid ecosystem changes (Scheffer et al. 2001; Kelly and Goulden 2008; Williams et al. 2013). For example, increased rates of background forest mortality (van Mantgem et al. 2009) and abrupt mortality events have been documented in a number of regions (Allen et al. 2010). Many tree species grow near their physiological moisture limits (Choat et al. 2012), and modeling experiments suggest that temperature-driven moisture stress will significantly alter forest composition and structure during the next century (Williams et al. 2013). However, few analogues for abrupt climate-driven forest changes exist in the historical record of the past few centuries, and longer-term perspectives can help characterize the spatiotemporal dynamics and potential likelihood of these events.

The paleoecological record is rich with examples of abrupt vegetation changes, although causes are still widely debated (e.g., Allison et al. 1986; Clark and Royall 1995; Shuman et al. 2004; Foster et al. 2006; Shuman et al. 2009; Booth et al. 2012a; Booth et al. 2012b). Much of terrestrial paleoecology has traditionally focused on millennial-scale responses of vegetation to climate change; however, finer temporal resolution is routinely

obtainable from many depositional archives, and the response of vegetation to sub-millennial climatic variability has received less attention. Understanding changes at decadal-to-centennial timescales may be especially relevant to forest management by identifying climatic and disturbance thresholds for abrupt forest change (Jackson and Hobbs 2009; Minckley et al. 2012). Recent developments in age-depth modeling techniques (e.g., Blaauw and Christen 2011), coupled with high-resolution analyses of both vegetation and climatic history, are poised to significantly contribute to our understanding of the drivers and spatiotemporal dynamics of past abrupt vegetation change, including assessments of temporal synchroneity and lags in response of vegetation to changes in climate and/or disturbance (Davis and Botkin 1985; Liu et al. 2012; Minckley et al. 2012; Booth et al. 2012a).

Peatland archives are one source of information on past environments, recording information on both the history of upland ecosystems, in the form of pollen and microscopic charcoal, as well as changes in the ecology and hydrology of the peatland itself. Ombrotrophic peatlands, those that derive all nutrients and moisture directly from the atmosphere are particularly sensitive to climate-induced changes in moisture balance (Charman et al. 2009; Booth 2010), and a range of techniques have been developed to estimate past surface-moisture conditions on these ecosystems using the peatland paleoenvironmental record (e.g., Booth 2008; Amesbury et al. 2012). Comparative studies of past surface moisture, upland vegetation, and regional fire history using these archives have proved to be valuable to the identification of linkages among climate, vegetation, and fire history at multidecadal-to-centennial timescales (e.g., Booth et al.

2012a and 2012b; Clifford and Booth 2013). Critical to this comparative approach is the analysis of climate, vegetation, and disturbance proxies from within the same depositional sequences, so that the relative timing and potential lags in vegetation response can be assessed with minimal chronological uncertainty.

Although numerous examples of abrupt vegetation changes exist in the paleoecological record (Foster et al. 1998; Booth et al. 2012a), only a few of these events have been carefully examined by comparison of vegetation, climate, and disturbance proxies within the same sediment cores (e.g., Booth et al. 2012b). For example, many pollen records from lakes and bogs in northeastern North America record shifts in forest composition between 500 and 600 yr BP; in fact, in New England the vegetation changes at this time were likely the largest and most widespread of the past millennium, except during post-settlement land clearance (Fuller et al. 1998). Relatively mesic species like Eastern hemlock (*T. canadensis*), beech (*F. grandifolia*), and sugar maple (*Acer saccharum*) decreased in abundance at many sites, while pine (*Pinus* spp.) and oak (*Quercus* spp.) increased during and after this time period (Fuller et al. 1998; Paquette and Gajewski 2013). The compositional changes that were initiated at this time persisted until European settlement.

A number of hypotheses have been put forward to explain the forest changes in the Northeast at this time, including Native American agricultural practices, climatic cooling associated with the Little Ice Age (LIA), drought, and/or fires – or some combination of all these mechanisms (Gajewski 1987; Campbell and McAndrews 1993; Shuman et al. 2009; Booth et al. 2012b; Paquette and Gajewski 2013). Testing these

hypotheses has been challenging, in part because few independent records of climate, fire, and vegetation exist with adequate temporal resolution to assess the relative timing of upland and climatic changes. Furthermore, similar vegetation changes were also observed between 500 and 800 years ago in portions of the central and western Great Lakes region (e.g., Gajewski 1987; Campbell and McAndrews 1993; Booth et al. 2012b), but it is unclear whether these changes were synchronous with those observed in the Northeast. The vegetation changes in the Great Lakes region were spatially heterogeneous, but drought and fire intolerant species like beech declined in portions of Michigan and southern Ontario at this time, similar to the patterns in the Northeast (Booth et al. 2012b). Recently, fire and drought have been implicated as likely triggers of these vegetation changes (Booth et al. 2012b), although cooler temperatures of the LIA have also been suggested (Gajewski 1987; Campbell and McAndrews 1993; Campbell and Campbell 1994; Paquette and Gajewski 2013). To determine whether the vegetation changes in the Great Lakes were synchronous with the changes in the Northeast requires precisely dated records and estimates of chronological uncertainty.

Recently, high-resolution analyses of microscopic charcoal and testate amoebae, a group of moisture-sensitive protists (Booth 2008; Mitchell et al. 2008; Booth 2010), from three Maine bogs indicated widespread drought and associated fires in southern and central Maine between 500 and 600 yr BP (Clifford and Booth 2013). In fact, this was the only time in the past 3000 years that concurrent drought and fire were recorded at all three bogs (Clifford and Booth 2013). Although the widespread drought and fires at this time may have caused the forest changes observed in regional pollen records, testing this

hypothesis requires a highly resolved comparison of drought, fire, and vegetation across this time period.

In this paper, we examined the forest transition that occurred between 500 and 600 yr BP in the Northeast, including the potential causes of this abrupt vegetation change and its timing relative to similar changes documented in the Great Lakes region. To do this, we first developed an observation-based hypothesis of the spatial patterns of the vegetation changes in the Northeast using available pollen records. We then tested the hypothesis that abrupt vegetation changes were driven by a combination of drought and fire by developing and examining reconstructions of bog surface-moisture estimated from testate amoebae, fire history inferred from charcoal analysis, and vegetation history inferred through pollen analysis. Each paleoecological proxy was sampled continuously in 1-cm intervals spanning the period of interest, so that the relative timing of events could be directly compared. Pollen-inferred changes in demography may be immediate or lagged in response to multidecadal environmental variability, because pollen-based inferences integrate the effects of mortality and recruitment of new individuals to pollen-producing age classes (e.g., Davis and Botkin 1985; Webb 1986; Jackson and Hobbs 2009, Minckley et al. 2012). Therefore, if drought and fire triggered the changes in forest vegetation between 500 and 600 yr BP, we expected stratigraphic evidence of drought and fire to occur synchronously with, or a few decades prior to, the vegetation changes. Finally, we use our data to compare the timing of the vegetation changes at well-dated sites in the Northeast with those from the Great Lakes region to assess whether the vegetation changes in the two regions were likely synchronous.

Study sites

Sidney Bog (44.39, -69.78) and Saco Bog (43.55, -70.46) are located in central and southern Maine, respectively, and are approximately 100 km apart (Fig 2.1a). Sidney Bog is located at an elevation of 91 meters, while Saco Bog is located at an elevation of 44 meters. Regional climate is classified as humid continental (Köppen, Dfb), and annual temperatures (~8^{o}C) and precipitation (119 cm at Saco, 106 cm at Sidney) are similar at the two sites. Both sites were glaciated, but were ice-free by at least 12,000 yr BP (Davis and Jacobson 1985). However, the upland soils surrounding Sidney Bog are comprised mainly of poorly sorted glacial till deposits (Maine Geological Survey, 2005), while the uplands surrounding Saco Bog are comprised of sand and fine grained sediments (Maine Geological Survey, 1999). The upland vegetation near Sidney Bog is currently classified as Laurentian-Acadian Northern Hardwoods Forest and Acadian Low-Elevation Spruce-Fir-Hardwood Forest (Gergely and McKerrow 2013), and upland forests surrounding the bog are dominated by hemlock, beech, sugar maple, and yellow birch (*Betula alleghaniensis*). Vegetation on the better drained soils surrounding Saco Bog is classified as a mixture of Central Appalachian Oak and Pine Forest and Northern Atlantic Coastal Plain Dry Hardwood Forest. Forests are dominated by several oak species, black birch (*Betula lenta*), white pine (*P. strobus*), and hemlock (Gergely and McKerrow 2013). Peatland vegetation found on both bogs was similar, with very scattered tree species including black spruce (*Picea mariana*), white pine, and tamarack (*Larix laricina*), with a typical peatland shrub complex comprised of Ericaceae species and a carpet of *Sphagnum*

moss. Saco Bog also contains several stands of Atlantic white cedar (*Chamaecyparis thyoides*).

Methods

Spatial patterning of forest change

To develop a regional perspective on the forest changes between 500 and 600 yr BP (where present was defined as the year 1950 AD) we used pollen records from the Neotoma Database (http://www.neotomadb.org/), including records from Connecticut, Maine, Massachusetts, New Hampshire, New Jersey, New York, Pennsylvania, Rhode Island, Vermont, and eastern Canada (Quebec, Nova Scotia, and New Brunswick). Datasets that resided in the database (as of 22 April, 2013), and the available pending datasets were used in the analysis. For the datasets that resided in the database we used sites and age-depth models developed by Blois et al. (2011), whereas for the pending data we used the Neotoma Database provided linear interpolation age-depth model for each site. For a site to be included in the synthesis it had to contain adequate sampling density, so only sites with >2 pollen samples in both a pre-transition (550-830 yr BP) and post-transition (250-530 yr BP) time period were used. The cutoff date of 250 yr BP was used to avoid the effects of European land-clearance (e.g., Fuller et al. 1998; Foster et al. 1998), and the window of 550-830 yr BP was chosen to be of the same length as the post-transition interval. Although Europeans settled some areas of the region as early as 400 yr BP, the regions around Sidney Bog and Saco Bog did not have permanent settlements until the mid-1700s AD (~200 yr BP) (Coolidge and Mansfield 1860). We also visually

inspected the pollen records to confirm that the *Ambrosia* spp. peak was not older than the inferred stratigraphic position of 250 yr BP. Twenty seven sites from the region were included in the analyses. Although many records from the region are not well dated, and therefore our resulting maps of vegetation change should be interpreted with caution, our intent was to provide an observation-based hypothesis of the spatial pattern of forest change across the time period of interest.

Multi-response permutation procedure (MRPP) was used to determine if forest community change between the two time periods was statistically different ($\alpha = 0.05$) at each of the 27 sites. MRPP is a non-parametric test used to determine how closely related groups consisting of multivariate data are to one another (Biondi et al. 1988). In order to standardize the application of MRPP among sites, 26 arboreal taxa were included in the analyses (Table 2.1). A Bray-Curtis (Sørensen) distance measure was used (Faith et al. 1987). In addition to examining the significance of pollen assemblage changes using MRPP, we also analyzed relative changes in pollen abundance from the pre-transition period to the post-transition period for several of the dominant tree pollen types in most records, including beech, hemlock, pine, and oak.

Paleoecological reconstructions

A wide-diameter piston corer (10.2 cm) equipped with a serrated end for cutting through peat was used to collect peat cores from Sidney Bog and Saco Bog (Wright et al. 1984). Field and laboratory methods were also described in Clifford and Booth (2013), as this study used the same cores as this previous work on drought and fire. Peat cores were

returned to the laboratory and cut into contiguous 1-cm intervals, and subsamples of 1 cm^3 were collected for testate amoebae, pollen, and microscopic charcoal analysis according to Booth et al. (2010). Samples were sieved and the fraction between 15 µm and 300 µm was kept for analyses. For testate amoeba analysis, a minimum of 100 tests was typically tallied in each sample and most tests were identified at a magnification of 400x. However, in a few samples the abundance of tests was quite low (6 samples out 61 samples between 250 and 550 yr BP), and only 50 tests were counted although this is typically sufficient for transfer function applications (Payne and Mitchell 2009). To reconstruct fire history and vegetation at each site, charcoal fragments and pollen between 15 µm and 300 µm were tallied on the same slides as the testate amoebae. A known number of exotic *Lycopodium* spores were added to each sample so that charcoal accumulation rates (CHAR) and pollen accumulation rates could be calculated. Pollen analysis followed standard procedures (Faegri and Iverson 1989) and counts were continued until at least 200 arboreal pollen grains were identified and tallied for each sample.

Water-table depths were reconstructed from testate amoeba assemblages using a weighted-averaging transfer function derived from 650 modern samples from North America, including Maine (Booth 2008). Standard bootstrapping techniques (n = 1000) were used to develop uncertainty estimates for water-table depth reconstructions. Although inferred water-table depths are sometimes detrended to remove millennial-scale patterns, because low frequency changes may be related to lateral bog expansion or other non-climatic developmental processes (Charman et al. 2006), we present raw water-table

depth reconstructions here because we focus on one time period and not the long-term trends. However, detrended versions of these two records can be found in Clifford and Booth (2013).

Timing and dynamics of drought, fire, and forest shifts

We developed age-depth models for both sites using an iterative Bayesian approach using the program Bacon (Blaauw and Christen 2011). Along with producing a best-fit age-depth model, the method results in multiple possible age-depth models given a set of *a priori* probability distributions describing the mean peat accumulation rate and "memory", which controls the flexibility of the age-depth model, so that temporal uncertainty at any point in the age-depth model can be estimated. To assess the timing of drought, fire, and vegetation changes during the time window of interest we assigned thresholds to objectively identify the depth of major events, where the onset of drought in the record was defined as the depth in the core where the change in the inferred water-table depth was greater than the root mean squared error (RMSEP) of the transfer function (i.e., a decrease of water-table depth of approximately >8.5 cm). Fire events were defined as those where the peak in charcoal influx exceeded 1.5 standard deviations above the mean charcoal influx (e.g., Clifford and Booth 2013). The timing of a decline or increase in a pollen type was defined as the age of the stratigraphic location where that taxon increased or decreased by 50%. To provide a better estimation of the amount of time between vegetation, fire, and drought events in each of the two records, we randomly selected 500 possible age-depth models for each site that were generated using

the iterative, Bayesian approach, and used these to develop probabilistic estimates of the amounts of time between the identified stratigraphic locations for drought, fire, and vegetation events.

Results and Discussion

Forest community shift between 500 and 600 yr BP

Over 74% of sites (20 sites out of a total of 27 examined) in the region recorded a significant change in pollen assemblages between the two time intervals, highlighting the widespread vegetation changes that were centered on 500 to 600 yr BP (Table 2). When the response of the dominant individual taxa (i.e., beech, hemlock, pine, and oak) were examined, 78% of sites recorded a >10% decrease in hemlock pollen, 80% of sites recorded a >10% decrease in beech pollen (Figure 2.1), and 88% of sites recorded declines of this magnitude in either beech or hemlock. Pine and oak increased at over 70% of sites across the time period. Fuller et al. (1998) noted that drier upland sites in New England that contained high percentages of oak pollen did not undergo major changes in forest composition at this time, and our results are consistent with this observation, as the ~20% of sites that did not record shifts in forest composition (Figure 2.1) tended to have higher percentages of oak. However, forest changes at this time occurred on both till and sandy soils, as evidenced by the records from Sidney Bog and Saco Bog (Figure 2.2).

Pollen records from Sidney Bog and Saco Bog were similar to other records in the region, with large declines in the pollen of more mesic taxa and increases in more

drought tolerant taxa between 500 and 600 yr BP. At Sidney Bog there was a 50% decline in hemlock and beech pollen, with a commensurate increase in pine and oak. Birch and spruce pollen percentages remained relatively constant during the record (Figure 2.S1and 2.S3). Similar patterns of vegetation change occurred on the better drained soils surrounding Saco Bog, where hemlock pollen declined and pine pollen increased dramatically. Prior to the vegetation change, forests surrounding Saco Bog were characterized by much more pine and oak than Sidney Bog (Figure 2.S2 and 2.S4), yet significant compositional changes still occurred. However, oak pollen percentages remained relatively stable across the transition and subsequently increased after European settlement. At both sites, the compositional changes between 500 and 600 yr BP persisted until European settlement, with hemlock and beech never regaining their pre-decline level of abundance (Figure 2.2).

Regional drought and fire between 500 and 600 yr BP

High resolution hydroclimate records derived from testate amoebae at Sidney Bog and Saco Bog both indicate that a severe and prolonged drought occurred between 500 and 600 yr BP. A similarly timed drought also has been documented at Great Heath Bog located 160 km to the east of Sidney Bog (Clifford and Booth 2013). During the drought event all three of these peatland sites recorded a large fire event, the only such time when all three records recorded both drought and fire during the last 3000 years (Clifford and Booth 2013). Furthermore, at Saco Bog the peatland itself burned at this time, depositing

a visible layer of charcoal and likely oxidizing pre-drought peat, resulting in a depositional hiatus between ~580 yr BP and ~1500 yr BP.

Temporal dynamics of drought, vegetation, and forest compositional change

The age-depth models for each site suggest variable rates of peat accumulation at both peatlands, with average deposition times at Sidney Bog and Saco Bog of 20 yr cm^{-1} and 7 yr cm^{-1}, respectively, which is within the expected accumulation rate of peatlands in the region (Goring et al. 2012). These accumulation rates provide adequate resolution for estimating the timing of abrupt events, and assessing the relative timing of fire, drought, and vegetation changes within the peat stratigraphy at each site.

The temporal sequence of drought, fire, and vegetation changes centered on 550 yr BP was similar at both Sidney Bog and Saco Bog (Figure 2.3). Vegetation changes at both sites likely occurred within a few decades following the onset of the drought and after the fire event. This lag is consistent with forest recovery after disturbance, as it would take several decades for newly recruited trees to enter pollen-producing age classes (e.g., Davis and Botkin 1985; Webb 1986). At Saco Bog a peatland fire removed a large portion of the record, making our interpretation of timing a bit more uncertain, but drought was still clearly indicated by very low water-table depths at and immediately after the depositional hiatus. Because of the hiatus, it is not possible to determine the exact timing of when the drought began, but we calculated the “drought onset” in the same manner as at Sidney Bog for consistency, and the vegetation clearly changed rapidly a few centimeters after (i.e., above) the hiatus.

Our records provide strong evidence that multidecadal drought and fire were both necessary to trigger the widespread vegetation change. For example, Sidney Bog recorded an earlier prolonged drought at 800 yr BP, but the forest composition did not change at this time. However, there was no evidence of fire associated with this drought event, suggesting that fire was important driver of forest change. Similarly, several earlier fire events were recorded in the Sidney Bog record, and although they were associated with relatively dry conditions, these droughts were not as severe and/or prolonged as the 500 to 600 yr BP drought.

Several other studies have suggested that temperature changes related to the LIA may have led to the observed abrupt and widespread vegetation changes at the time (e.g., Fuller et al. 1998; Paquette and Gajewski 2013), and while our new records do not directly reject this hypothesis they do provide strong evidence for drought and fire playing a major role. When the timing of the drought, the associated fire events, and the changes in forest taxa are compared to the timing of the LIA temperature changes from the Northern Hemisphere, our data show that these ecological events also probably occurred prior to the cooling of the LIA (Figure 2.4). However, temperature reconstructions from the Northern Hemisphere may not be representative of the timing of temperature changes in the Northeast, and unfortunately, no high-resolution, vegetation-independent records of temperature exist for the region. Although temperature-related changes may have influenced post-disturbance recovery patterns, and possibly contributed to the long-term persistence of the compositional changes, our records clearly

identify drought and fire as the likely proximate drivers of the abrupt and widespread vegetation change.

Forest compositional changes persisted until European settlement (e.g., Figure 2.2), and secondary succession after the drought and disturbance did not return the system to its pre-disturbance composition. This pattern highlights the potential for transient climate and disturbance events to leave long-term legacies at landscape-to-regional spatial scales. The cause of the persistence of the forest changes are unclear; however, post-fire recruitment would have occurred during unusually dry conditions, favoring species with drought-tolerant seedlings and saplings, and once the forest canopy regenerated, positive feedbacks (e.g., altered microclimate, seed influx) likely maintained a relative stable forest composition (e.g., Nowacki and Abrams 2008). Alternatively, cross-scale interactions, such as the combination of multidecadal drought and fire with lower-frequency temperature changes associated with the MCA-LIA transition, may have influenced post-disturbance forest succession (e.g., Ibanez et al. 2007; Vitasse et al. 2012), favoring the recruitment of pines and oaks over hemlock and beech. The LIA climate of the Northeast may have been particularly favorable for pine and oak species; however, the drought and disturbance event were likely necessary to push the system into a new stable state that persisted until European land-clearance. (e.g., Overpeck et al. 1990; Beisner et al. 2003).

Timing of forest changes across eastern North America

The drought and vegetation changes in the Northeast likely occurred several centuries after similar changes occurred in the Great Lakes region (Figure 2.4). For example, a series of drought and fire events recorded at Minden Bog and Irwin Smith Bog in Lower Michigan, were linked to the regional decline of beech populations, and associated expansion of pine and oak, between 700 and 800 yr BP (Booth et al. 2012b). However, comparing the estimated timing of vegetation changes and drought events in the two regions indicates little overlap in age estimates, suggesting that they represent vegetation responses to different events (Figure 2.4). Droughts and fires during Medieval Climate Anomaly, which extended from the midcontinent to the western USA (Cook et al. 2007), were likely associated with the vegetation changes in the Great Lakes region, whereas the drought and vegetation changes in the Northeast appear to have occurred several centuries later. However, given that both regions experienced major drought-induced forest changes during the past millennium, our records highlight the potential of droughts and associated disturbances to lead to abrupt and persistent ecological change. The role of drought in triggering widespread forest change in humid regions like eastern North America has been underappreciated, likely because severe, multidecadal droughts have not been common during the past century in these regions.

Conclusions

Recent climate-induced forest mortality and rapid compositional change, particularly in semi-arid regions, and projected increases in the frequency of extreme climate-driven vegetation shifts have highlighted the need to better understand both short and long-term

dynamics of such events (Allen et al. 2010; Williams et al. 2013). The widespread changes in forest vegetation that occurred in the Northeast between 500 and 600 yr BP were likely driven by a regional, multidecadal drought and associated fires, similar to the forest changes that occurred in the Great Lakes region several centuries earlier (Booth et al. 2012b). Our coupled records of past hydroclimate, fire, and vegetation indicate that the paleoecological record is well suited to examine the characteristics of abrupt vegetation changes on multidecadal timescales relevant to resource management (e.g., Foster et al. 2006; Shuman et al. 2009; Booth et al. 2012b).

Our records from Maine add to a growing body of evidence indicating that forested ecosystems in humid regions are sensitive to moisture variability and may undergo rapid, widespread, and long-lasting compositional change in response to transient drought and fire events (Pederson et al. 2014). Although the rapid forest changes between 500 and 600 yr BP were likely triggered by transient drought and fire, post-fire succession occurred in the context of more gradual temperature changes associated with the LIA-MCA transition. Ongoing and future ecological changes in the region may exhibit similar characteristics, with disturbances linked to decadal-to-multidecadal drought variability, and subsequent forest recovery and gap dynamics occurring during a time of increasing temperatures. Some regional climate projections suggest that warming temperatures may be associated with increased precipitation and drought variability (Hayhoe et al. 2007), and our records suggest that this potentially increases the likelihood of rapid and widespread vegetation change (e.g., Mohan et al. 2009). Much work is needed to more fully incorporate paleoecological perspectives on

abrupt vegetation changes into vegetation models and resource-management decisions (Jackson and Hobbs, 2009; Vegas-Vilarrubua et al. 2011), including efforts to estimate wildfire risk (United States Forest Service, 2010). However, long-term perspectives will continue to improve our understanding of the factors and feedbacks that control forest resilience (Reyer et al. 2015), and when coupled with taxa specific bioclimatic and physiological thresholds of tree mortality, will contribute to the development of necessary, and realistic models of forest change under variable and changing climatic conditions.

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Table 2.1. List of pollen taxa used in community regional analysis.

Taxa Name
Abies
Acer
Betula
Carya
Castanea
Cornus
Corylus
Cupressaceae
Fagus
Fraxinus
Juglans
Larix
Liriodendron
Liquidambar
Nyssa
Ostrya
Picea
Pinus
Platanus
Populus
Prunus
Quercus
Taxodium
Tilia
Tsuga
Ulmus

Table 2.2. Sites and Multiresponse Permutation Procedure (MRPP) statistics used in the regional analysis of forest community change. Site number corresponds to numbers in Fig. 2.2 and **bold** P-values are significant at $\alpha = 0.05$.

Site no.	Site name	Citation	pre-transition (n)	post-transition (n)	MRPP	A
1	Aino Pond	Fuller et al. (1998)	10	11	**P < 0.001**	0.173
2	Balsam Lake	Ibe (1982)	4	4	**P < 0.05**	0.106
3	Basin Pond	Gajewski (1987)	9	7	**P < 0.001**	0.156
4	Big Reed Pond Hollow	Schauffler and Jacobson, Jr. (2002)	3	4	**P < 0.01**	0.319
5	Conroy Lake	Gajewski (1987)	7	7	**P < 0.01**	0.183
6	Deep Pond	Parshall and Foster (2002)	5	6	P = 0.10	0.044
7	Duarte Pond	Foster et al. (2002)	9	8	P = 0.09	0.038
8	Ely Lake	Gajewski (1987)	5	4	**P < 0.05**	0.088
9	Green Pond	Fuller et al. (1998)	9	14	**P < 0.01**	0.053
10	Harlock Pond	Foster et al. (2002)	4	4	P = 0.48	-0.008
11	Lake Pleasant	Fuller et al. (1998)	5	3	P = 0.52	-0.010
12	Lily Warwick	Fuller et al. (1998)	10	9	**P < 0.001**	0.413
13	Linsley Pond	Brugman (1978)	9	9	**P < 0.01**	0.059
14	Little Bolton	Fuller et al. (1998)	8	8	**P < 0.05**	0.046
15	Little Mirror Lake	Fuller et al. (1998)	9	7	**P < 0.01**	0.081
16	Mansell Pond	Almquist-Jacobson and Sanger (1995)	4	5	P = 0.81	-0.044
17	North Round Pond	Francis and Foster (2001)	7	5	**P < 0.01**	0.100
18	Otter Pond	Fuller et al. (1998)	7	8	**P < 0.01**	0.090
19	Pecker Pond	Francis and Foster (2001)	3	3	**P < 0.05**	0.230
20	Piermont Marsh	Pederson et al. (2005)	9	9	**P < 0.01**	0.059
21	Quag Pond	Fuller et al. (1998)	8	7	**P < 0.001**	0.128
22	Saco Bog	This study	4	8	**P < 0.001**	0.312
23	Sidney Bog	This study	6	9	**P < 0.001**	0.307
24	Silver Lake (MA)	Fuller et al. (1998)	22	5	**P < 0.05**	0.035
25	Silver Lake (PA)	Russell et al. (1993)	4	3	P = 0.09	0.059

26	Snake Pond	Fuller et al. (1998)	3	5	P = 0.09	0.112
27	South Bog	Dieffenbacher-Krall (1996)	3	5	**P < 0.05**	0.254

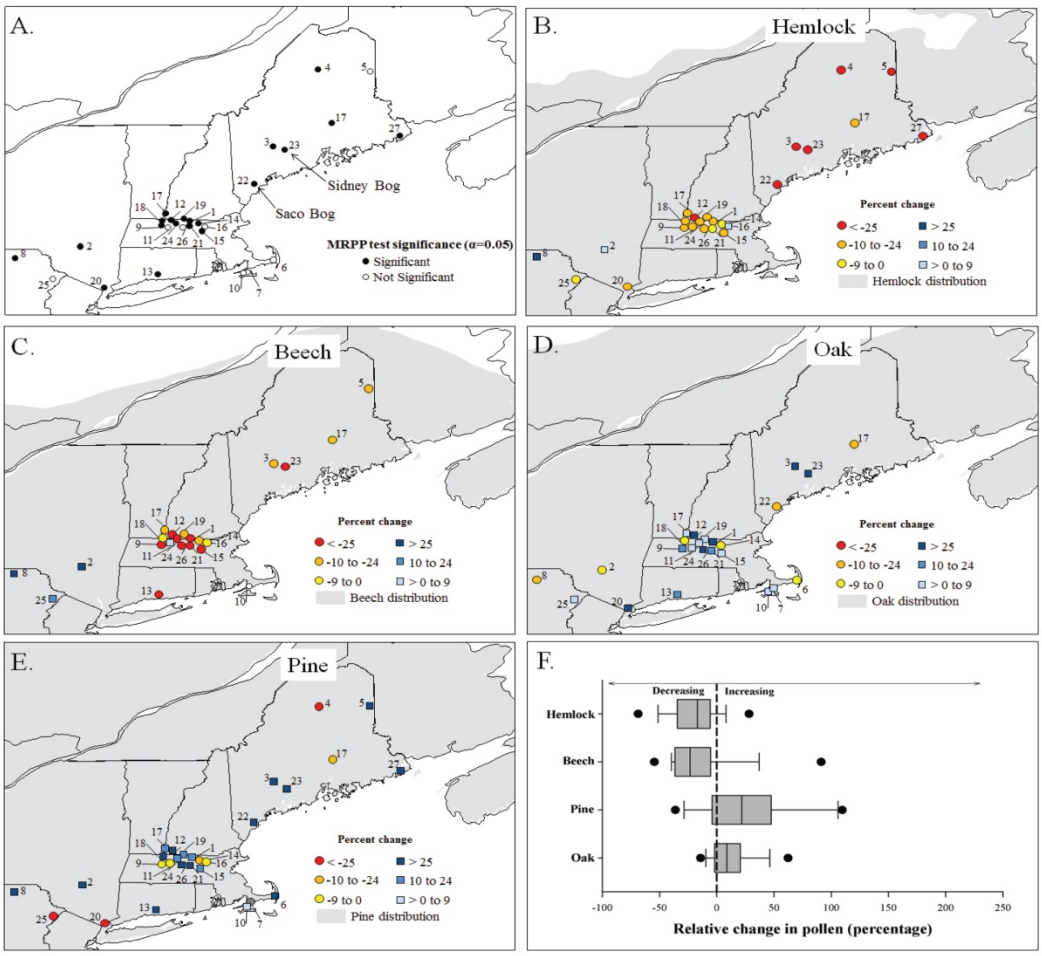

Figure 2.1. A) The location of sites used in the regional pollen synthesis and significance of pollen changes between two temporal windows (250-530 yr BP and 550-830 yr BP). Closed circles show sites that had significantly different arboreal pollen percentages between pre-transition and post-transition time periods. The numbers correspond to the site numbers in Table 1. Change in pollen percentages between pre-transition and post-transition time periods for B) hemlock, C) beech, D) pine, and E) oak. Only sites where >5% arboreal pollen was comprised by each taxon are shown. F) Boxplots showing the changes in relative pollen percentages among all sites across the two time windows.

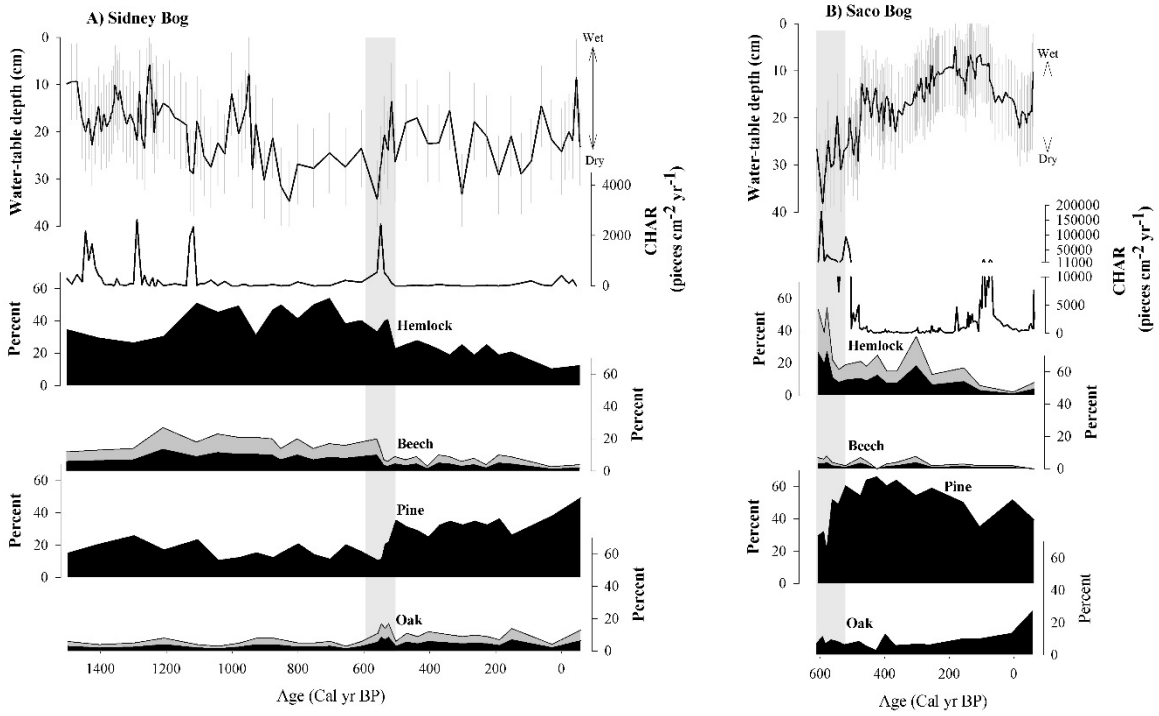

Figure 2.2. Water-table depth, fire, and dominant pollen changes at A) Sidney Bog and B) Saco Bog. A depositional hiatus (peatland fire) at Saco Bog occurred at approximately 600 yr BP, and no record exists between 600 and 1500 yr BP. Gray shading on pollen diagrams represents 2-times exaggeration and gray vertical bars highlight the timing of vegetation transition (500 to 600 yr BP) in both records.

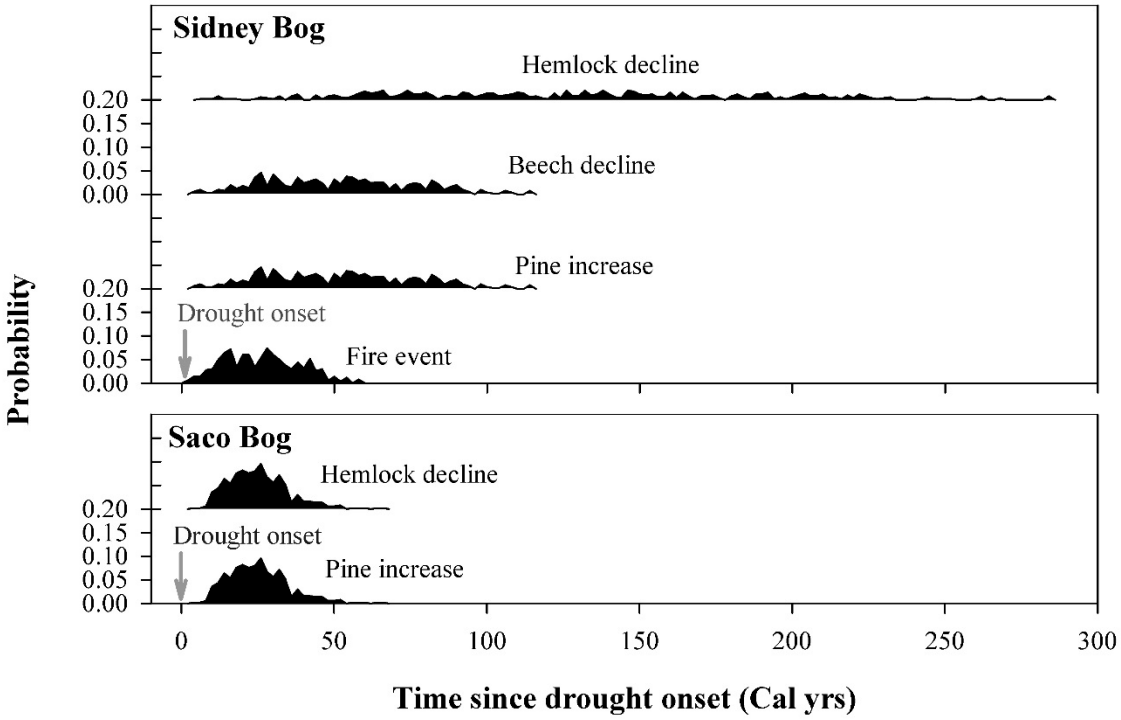

Figure 2.3. The timing of fire onset, declines in hemlock and beech pollen, and increases in pine pollen relative to the onset of drought for both Sidney Bog and Saco Bog. Time 0 represents the onset of the drought. The probabilty distributions of the lags in response of fire and vegetation to the drought were developed using 500 possible age-depth models at each site. For these analyses, the onset of fire and drought were assumed to be synchronous at Saco Bog, where the peatland burned.

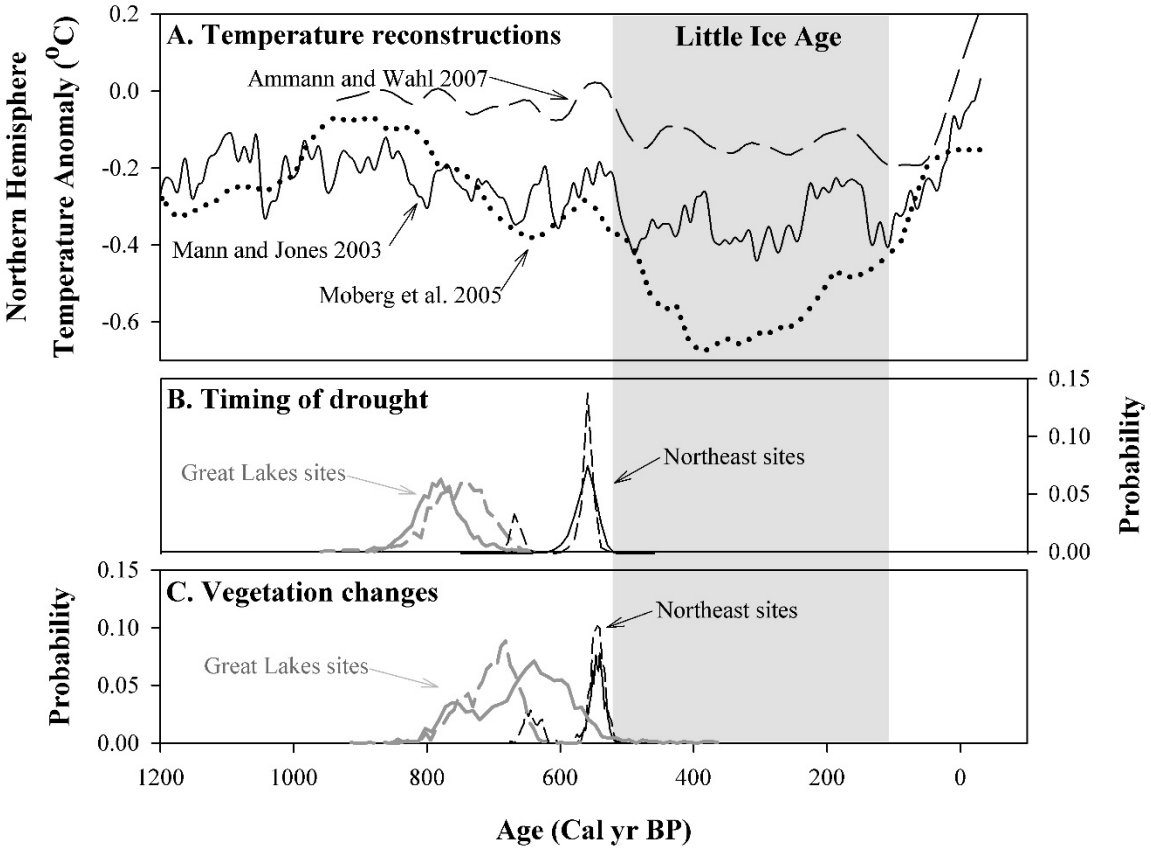

Figure 2.4. A) Northern Hemisphere temperature anomaly from Mann and Jones (2003), Moberg et al. (2005), and Ammann and Wahl (2007). B) Comparison of the timing of drought at two Northeastern sites (Sidney Bog – black, dashed line and Saco Bog – black, solid line) and two sites from the Great Lakes (Minden Bog – gray, solid line and Irwin Smith Bog – gray, dashed line; Booth et al. 2012b). C) The timing of vegetation changes at two sites in the Northeast and two sites in the Great Lakes, both lag the onset of drought, and in the Northeast where the age-depth models are based on more ^{14}C dates this lag was likely a couple decades long.

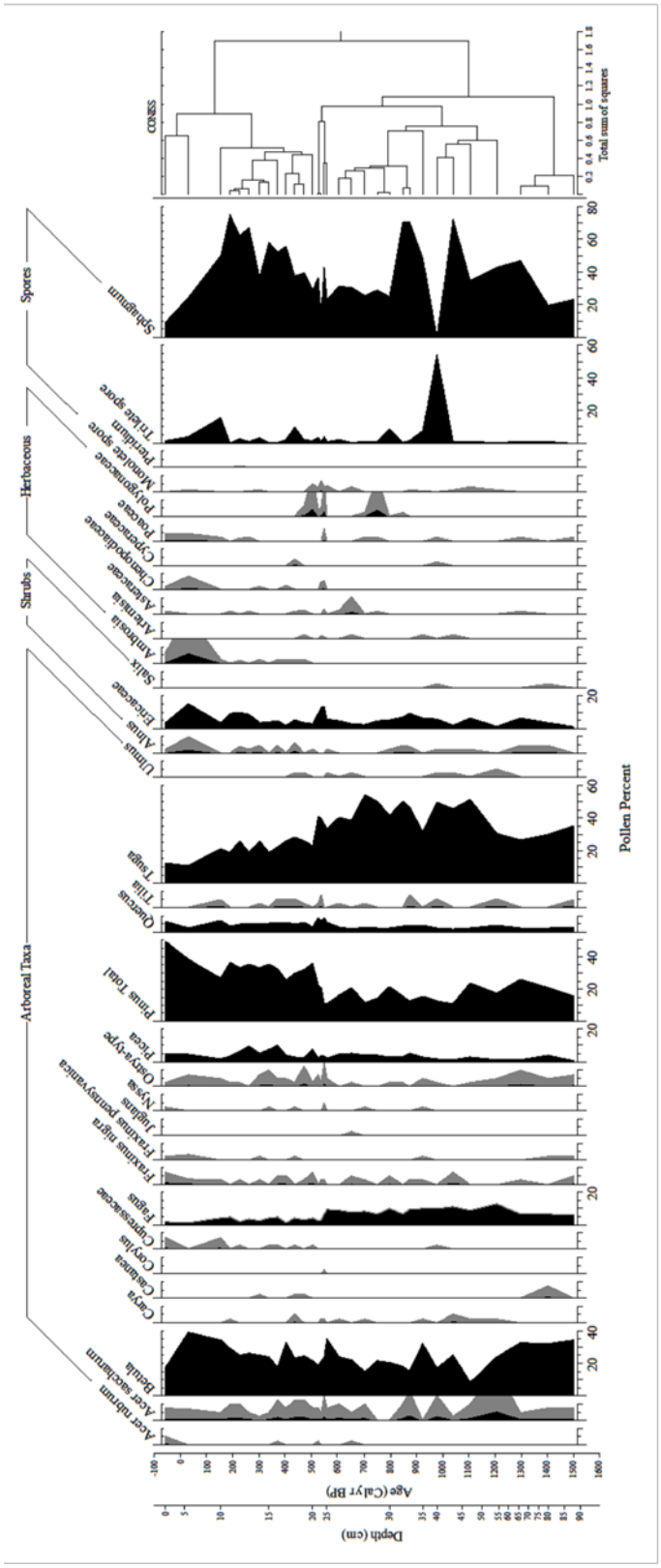

Figure 2.S1. Pollen percentage diagrams for Sidney Bog. Gray shading is 5-times exaggeration.

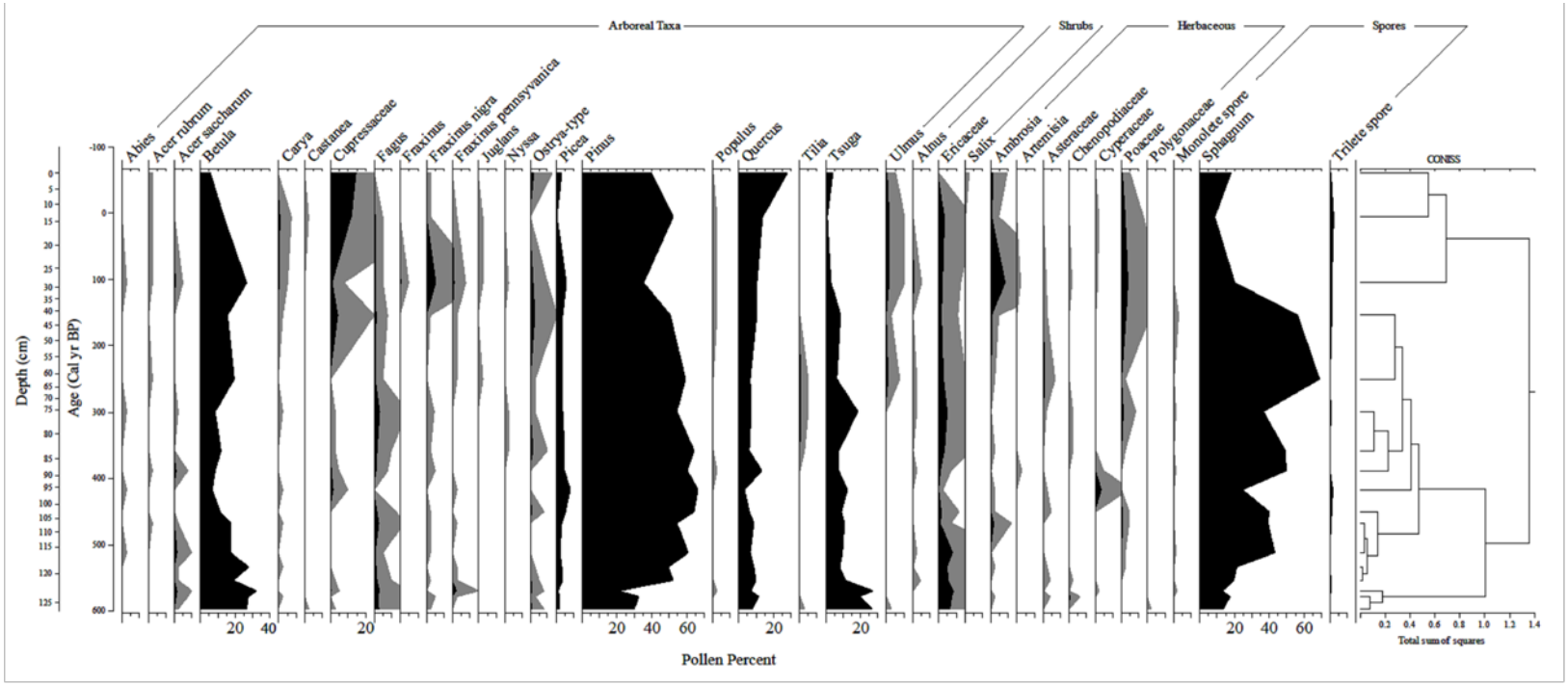

Figure 2.S2. Pollen percentage diagrams for Saco Bog. Gray shading is 5-times exaggeration.

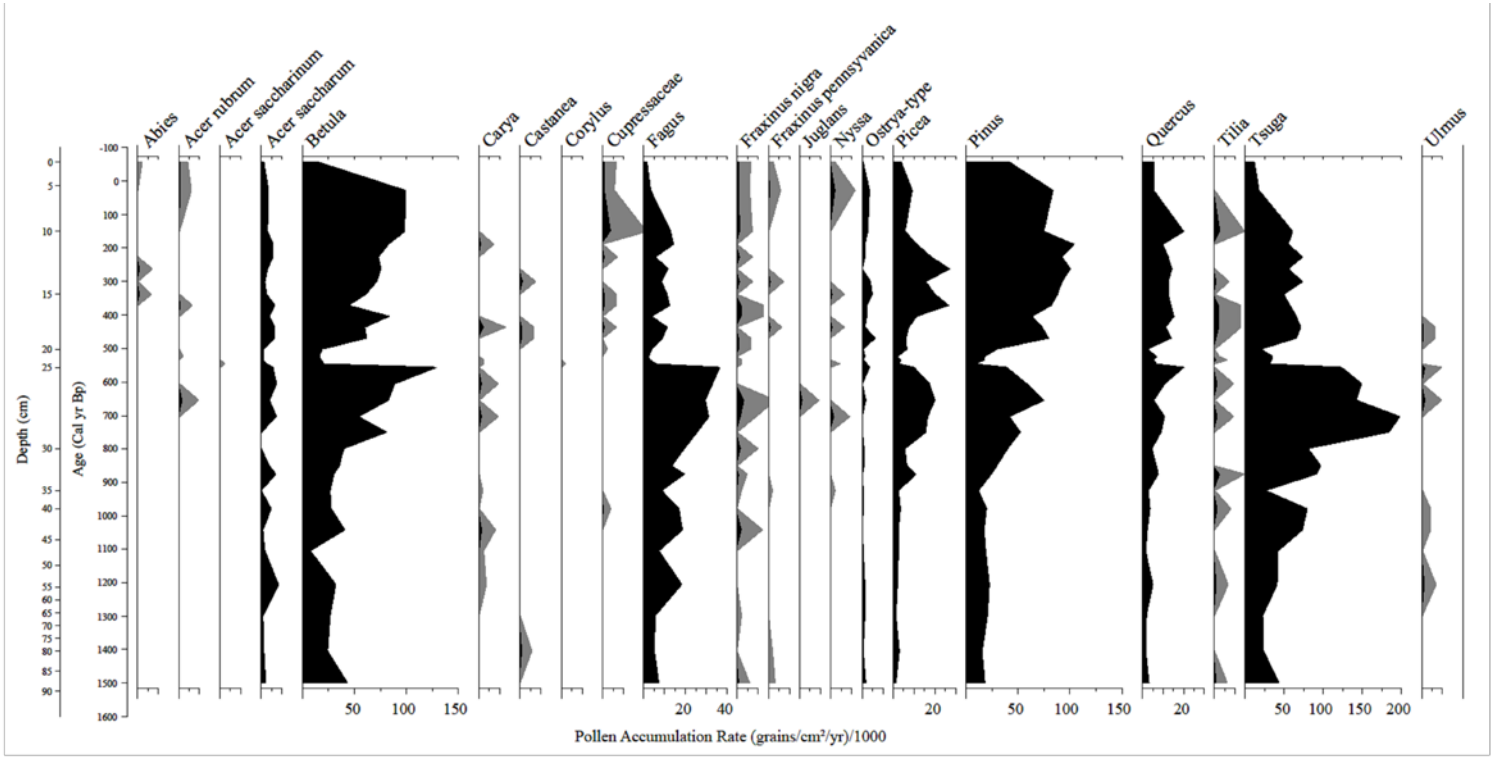

Figure 2.S3. Pollen accumulation rates of arboreal taxa at Sidney Bog. Gray shaded areas are 5-times exaggeration. All data are divided by 1000 to fit on the plot. Note x-axes scale for each taxa are different so that they fit appropriately.

A multiproxy, event-based stacked record of late Holocene hydroclimate from New England

Introduction

The development of regional paleoclimate records from multiple sites provides replication and an assessment of whether climate proxies respond to the same climatic drivers, and to what extent they record a regional climate signal – rather than local or autogenic processes (e.g., Charman et al. 2006; Nelson et al. 2006; Blundell et al. 2008; Swindles et al. 2013). However, aside from climate records derived from tree rings or varved lake sediments, the chronologies of most proxy-climate records are based on radiometric dating techniques with considerable age uncertainties, making the comparison and compilation of multiple, non-annually resolved paleoclimate proxies difficult (Blackford 2000; Charman et al. 2006). Techniques for "stacking" or "compiling" such paleoclimate records have typically involved tuning chronologies, often by assuming that extreme events are synchronous among sites and using these events as chronological markers (e.g., Charman et al. 2006; Swindles et al. 2012a). Although recent studies have demonstrated potential pitfalls associated with chronological tuning (e.g., Blaauw 2012; Swindles et al. 2012a), comparisons between tuned and non-tuned records often suggest similar patterns (Swindles et al. 2012a). Recent advances in age-depth modeling techniques allow for better estimates of age uncertainties and improved methods for examining relationships among sites (e.g., Blaauw et al. 2007; Blaauw and

Christen 2011), potentially facilitating better integration of records from multiple sites in a region.

Most lake and peatland-derived paleohydrological records are developed as continuous time series of moisture proxies (e.g., Charman et al. 2006; Nelson et al. 2006; Swindles et al. 2013; Newby et al. 2014). Peat-based records may be particularly good recorders of multidecadal extreme events, whereas some of the lower magnitude and lower frequency trends in these records may be due to autogenic processes such as ecohydrological feedbacks, vertical peat growth, changes in hydraulic conductivity, and other ecological dynamics (Charman 2002; Charman et al. 2006; Swindles et al. 2012b; Waddington et al. 2015). Surface moisture conditions of ombrotrophic peatlands, which receive all of their nutrients and moisture from precipitation, are sensitive to regional climatic conditions (Charman et al. 2009; Booth 2010; Amesbury et al. 2012; Barber et al. 2013). Evidence further suggests bog surface-moisture responds predominantly to summer, or growing season, precipitation (Charman et al. 2004; Charman et al. 2007; Charman et al. 2009; Booth 2010), and a range of surface-moisture proxies have been developed in these ombrotrophic peatland systems (Blackford 2000; Booth 2002; Hughes et al. 2006).

Water-table depth reconstructions based on changes in the community composition of testate amoebae, a group of moisture-sensitive protists that produce decay-resistant shells, have been most widely applied (e.g., Booth 2002; Booth 2008; Mitchell et al. 2008). Testate amoebae-inferred water-table depth reconstructions have been validated against the instrumental climate record and via comparison with other

moisture proxies within and among sites (Charman et al. 2009; Booth 2010; Amesbury et al. 2012). While it is likely that variability in the reconstructed surface-moisture proxies includes some autogenic signals (e.g., Swindles et al. 2012b; Waddington et al. 2015), utilizing a network of sites and proxies derived from both the peatland and upland environments (e.g., Clifford and Booth, 2013) should highlight the extreme climatic-driven events (Charman et al. 2006; Swindles et al. 2013).

The development of stacked water-table depth records has been done in several peat-rich regions, such as the United Kingdom (e.g., Charman et al. 2006; Blundell et al. 2008; Swindles et al. 2010; Langdon et al. 2012; Swindles et al. 2013). For example, Swindles et al. (2013) showed good coherence among many peatland-derived testate amoeba records in the United Kingdom compared to lake and speleothem moisture-balance reconstructions. While stacked peatland records have been developed throughout parts of the United Kingdom, none have been developed in North America. Testate amoebae-derived water-table depth records have been developed for eastern North America (e.g., Booth et al. 2006; Hughes et al. 2006; Clifford et al. 2013), and have been linked with fire and vegetation records to provide important insights into regional-scale forest responses to past moisture variability (Booth et al. 2012a, 2012b, Clifford and Booth 2013). A composite peat-derived paleoclimate record would have considerable value in global change studies, particularly in densely populated northeastern North America, which has experienced a dramatic increase in precipitation over the past half-century (Pederson et al. 2013). This recent increase in regional moisture balance, as well as projections of more varied climate and increased probability of drought events under

future warmer climate conditions (Hayhoe et al. 2007), highlights the need for long-term perspectives on moisture balance (Collins et al. 2013).

In this study, I developed a composite multiproxy surface-moisture record from three peatlands in Maine using water-table depth reconstructions and peat humification. I employ a new approach that focuses on the identification of extreme dry and wet events (> 1 standard deviation from mean) using multiple proxies from multiple sites, while characterizing the chronological uncertainty of these events. By focusing on extreme events that are replicated among sites, the resulting reconstruction is a conservative estimate of past prolonged and high magnitude multidecadal changes in moisture variability that is less susceptible to autogenic influences and some of the issues inherent in stacking continuous records (Charman et al. 2006; Langdon et al. 2012; Swindles et al. 2013).

Methods

Field collection and laboratory analyses

Peat cores were collected from three raised, ombrotrophic *Sphagnum*-dominated peatlands in Maine (Figure 3.1) using a wide-diameter modified Livingstone piston corer. Field and laboratory methods were detailed in previous papers (Clifford and Booth 2013; 2015) so are only briefly described here, and identical methods were used for all three sites. Cores were cut into 1-cm sections for subsampling of testate amoebae, which were processed and analyzed using standard methods (Booth et al. 2010). Water-table depth reconstructions were performed using a weighted average transfer function comprised of

650 calibration samples from North America and associated water-table depth measurements (Booth 2008; Markel et al. 2010). However, the taxa *Difflugia pristis* was removed from the transfer function as there is little modern data. For analyses of peat humification, peat subsamples of 3 cm^3 were dried and ground into a fine powder treated with 8% NaOH, lightly boiled, and then filtered using standard procedures (Chambers et al. 2011). Light transmittance was measured at 540 nm using a spectrophotometer. At one site, Great Heath, alkane biomarkers were used to calculate a *Sphagnum* to vascular plant ratio (SVR) in a previous study (Nichols and Huang 2012), and I compare my data to these measurements. At all sites charcoal particles between 15 µm and 300 µm in size were counted on testate amoebae slides, and concentrations were calculated with a known number of *Lycopodium* spp. marker spores (e.g., Clifford and Booth 2013).

Age-depth models

Age-depth models were developed using a flexible Bayesian modeling framework using the program 'Bacon' (Blaauw and Christen 2012). An iterative process developed >100,000 age-depth models, and these were used to estimate a most probable age-depth model. Age-depth models were developed using a set of *a priori* probability distributions, such as mean accumulation rate, "memory" (i.e., autocorrelation between steps), and step size – all of which can influence the flexibility of the age-depth model. Age-depth models were optimized for each site individually, by changing the *a priori* probability distributions for mean accumulation rate, which was estimated by using linear regressions through the midpoints of the calibrated radiocarbon dates (Clifford and Booth 2013).

Additionally, memory was left at the default value for strength and mean of 4 and 0.7, respectively. Step size was set at the default of 5 cm for Sidney Bog and Great Heath, but was set at 4 cm for Saco Bog to better fit the length of the core so that each centimeter (i.e., sample) was included. Radiocarbon dates were calibrated using the IntCal09 curve (Reimer et al. 2009). At Saco Bog, a hiatus occurred due to a fire on the peatland, leaving a visible charcoal layer (Clifford and Booth 2013, 2015), and radiocarbon dates bracketed the approximately 1000 year hiatus, with one date just above the charcoal-inferred hiatus and another one 10 centimeters below. To model the ages for the 10 cm of peat below the charcoal layer, a linear interpolation of the best-fit model was extrapolated upward across the 10 centimeters to the position of the charcoal-inferred hiatus.

Examination and analyses of proxy climate records

Pearson's correlations were used to assess relationships between water-table depth, humification, and SVR (at Great Heath) within each record. Correlations were performed on raw and detrended datasets, to assess the potential effects of detrending on correlation structure. Pearson's correlations were also performed along running windows to examine relationships among proxies through time. These running correlations were performed via depth (as opposed to time) but sample sizes were chosen to reflect an average window-size of 400 years at each site, which corresponded to a different number of samples (depths) at each site because of the different accumulation rates at the three sites (e.g., Sidney Bog was 21 cm yr^{-1}, Great Heath was 51 cm yr^{-1}, and Saco Bog was 61 cm yr^{-1}).

Identification of large wet and dry events

Large magnitude wet and dry events were identified using water-table depth reconstructions, and humification data were used to assess confidence in these identifications. Charcoal accumulation rate (CHAR) peaks were also used to provide additional evidence for the inference of dry events. Given the lack of correlation between SVR and other proxies at Great Heath (see results), the SVR reconstruction was not used for identification of large wet and dry events. Large wet and dry events were identified in the water-table depth record if they were >1 or <-1 standard deviation from the mean (for dry or wet period, respectively). Humification support for the water-table depth inferences was interpreted if there was an increase or decrease >1 standard deviation between adjacent samples in the humification record at the same depth, or within 1 cm of a wet or dry event inferred from the water-table depths. Humification changes that occurred in adjacent centimeters to those inferred from water-table depths were considered the same events because of the potential for short lags in the response of decomposition to moisture changes and the possibility of secondary decomposition (Borgmark and Schoning 2006; Morris et al. 2015). For events spanning multiple centimeters, timing was estimated using the average of the mean ages for these centimeters and the low and high bounds from the included centimeters was used to characterize the uncertainty. Using the three proxies, three levels of confidence were inferred for the dry events in the water-table depth record: 1) all measured proxies recorded the event (i.e., testate amoebae, humification, charcoal), 2) two proxies recorded

the event (i.e., testate amoebae, and humification or charcoal), and 3) only testate amoebae. For wet events, only two proxies were used, testate amoebae and humification.

Stacking and compilation of multiproxy records at multiple sites

Multiple proxy records (i.e., testate amoebae, humification, and charcoal) from the three sites were used collectively to identify the history of high-magnitude, regional moisture fluctuations. The records were stacked using the methodology of Charman et al. (2006), where all water-table depth records were detrended to remove multi-millennial scale trends, and a multidecadal LOESS (locally weighted scatterplot smoothing) curve was fitted to the residuals from all sites. In addition to this approach, several other record stacking techniques were explored to better understand the timing of extreme events and assess the robustness of the reconstructions. These techniques included a weighted stacking of extreme events, where the stacked record was weighted based on number of proxies that recorded the same event within each site. Additionally, a 400-year running sum of extreme events was performed, where each dry and wet event was summed and binned by time. For the running sums of extreme events, each proxy record and site was placed on the same time-scale, so differences of time resolution did not create a bias. Finally, probability distributions of the timing of dry and wet events using the chronological uncertainty in the age-depth model were developed for each site. Probability distributions of the timing for each event were extracted from the iterative Bayesian age-depth model to develop a probabilistic estimate to examine the timing of extreme events among sites. The probability distributions for each site were also

compiled into a single record showing the regional probability of occurrence of either dry or wet events. Probability distributions of the timing of dry and wet periods for each site were compiled into a regional record summarizing the multi-site probability of the timing of dry and wet events. To be considered synchronous, events needed to occur at multiple sites and have > 5% overlap of the probability distributions, with the assumption that < 95% difference was statistically the same at $\alpha = 0.05$, so that the event was considered the same among sites.

Results

Age-depth models

Age-depth models (Figure 3.2) show average peat accumulation rates were similar to regional expectations (e.g., Goring et al. 2012), but varied among sites (e.g., Sidney Bog: 20 year cm^{-1}, Great Heath: 11 year cm^{-1}, and Saco Bog: 7 year cm^{-1}) and along the length of the cores. It should be noted that only the upper portions of the cores were examined in this study. Note differences in age-depth model at Great Heath compared to Nichols and Huang (2012), as here the age-depth model was developed with radiocarbon dates from the first 100 cm, rather than the entire length of the sediment core. The short age-depth model was used because of potential gaps in the sediment record between core drives that may have occurred during fieldwork. At Saco Bog the record was not likely continuous as a visible charcoal layer was deposited from a peat fire and radiocarbon dating indicates unrealistic slow accumulation rates (Goring et al. 2012; Figure 3.2).

Proxy records and comparisons within each site

Testate amoeba community composition varied considerably with depth in the three cores (Figure 3.3, 3.4, 3.5). Inferred dry and wet time periods, in both raw and detrended reconstructions, were generally caused by the abundance of similar taxa among sites. For example, taxa most associated with dry intervals included *Hyalosphena subflava*, *Trigonopyxis arcula*, and *T. minuta* (Figure 3.3, 3.4, 3.5). The taxa most associated with pluvials were *Archerella flavum* and *Arcella discoides*. At Great Heath and Saco Bog the taxa *Heleopera sphagni* and *Hyalosphia elegans* were also present during wet time periods, but typically composed less than 10% of the community. At Sidney Bog, *A. discoides* was the dominant taxon during most inferred wet periods, as *A. flavum* was only present during the time period of 1300 Cal yr BP to 1900 Cal yr BP. All of these taxa are well-known indicators of surface-moisture conditions, although abundant *A. discoides* may also suggest highly variable conditions (Booth 2002; Booth 2008; Sullivan and Booth, 2011). *Difflugia pristis*-type, a morphological grouping that may consist of various taxa and is not well represented in modern samples, ranged from present to common at each site. Because of the poor representation in modern samples, and uncertain ecology of this taxon, *D. pristis* was not included in relative abundance calculations for the reconstruction of water-table depth at the sites.

Inter-proxy comparisons at Sidney Bog provide support for the interpretation of surface-moisture as a major driver of testate amoeba community change, and provide increased confidence in the water-table depth reconstruction. The overall correlation

between water-table depth and humification records at Sidney Bog was r = 0.25, and throughout the record the correlation between these two proxies was always positive at multi-century timescales (Figure 3.6) and for much of the record these correlations were significant, where $\alpha = 0.1$ and 0.05. Furthermore, where the correlations were weakest the two proxies appear to be offset by small lags, such as during the fluctuations between about 1500 Cal yr BP and 1000 Cal yr BP. Removal of multi-millennial patterns through detrending the proxy records had little effect on the correlation (r = 0.24). High magnitude fluctuations were also generally well replicated by the proxies, with some of the largest drying events centered on 550 Cal yr BP, 1050 Cal yr BP, 1250 Cal yr BP, and 1400 Cal yr BP (Table 3.1). Large wet events recorded in both proxy records occurred 350 Cal yr BP, 1250 Cal yr BP and 1500 Cal yr BP. The microscopic charcoal record indicated six significant peaks in upland fire activity and all were associated with dry conditions; four peaks occurred synchronously with drying events in both humification and testate amoeba reconstructions (550 Cal yr BP, 1050 Cal yr BP, 1300 Cal yr BP, and 1400 Cal yr BP), and two charcoal peaks occurred during large drying events indicated by testate amoebae alone (1850 Cal yr BP and 2700 Cal yr BP).

Comparison of humification and water-table depth records at Great Heath indicated a similar level of agreement between these two proxies (overall r = 0.39) as that observed at Sidney Bog, with a positive correlation at multi-centennial timescales throughout the record, almost all of which was statistically significant at the 0.05 and 0.1 alpha levels, although this does not account for autocorrelation (Figure 3.7). However, the SVR record was not correlated with the other two proxies (Figure 3.7). Detrending

caused a slight decrease in the overall correlation between humification and water-table depth ($r = 0.30$) and did not improve the correlation with SVR. Both water-table depth and humification indicated drying events centered at 150 Cal yr BP. In addition, a drying event was suggested by humification at approximately 350 Cal yr BP, and was shortly followed (within decades or 6 cm of core depth) by a testate amoeba-inferred drying event, suggesting the possibility of secondary decomposition. Although poorly correlated with the other proxies overall, SVR suggests expansion of vascular plants relative to *Sphagnum* at 550 Cal yr BP and 150 Cal yr BP indicating drying during these time periods. Humification indicates a few transient fluctuations, not associated with inferred water-table depth changes, between 500 and 460 Cal yr BP. Large wetting events were indicated by both humification and testate amoebae at 900 Cal yr BP, 530 Cal yr BP, and 380 Cal yr BP. There were four microscopic charcoal peaks and all were associated with dry conditions; three of them occurred synchronously with dry periods in the water-table depth record, and a charcoal peak at 550 Cal yr BP occurred when both humification and water-table depth records indicated a dry period. Due to the lack of correlation between SVR and the other proxies, the SVR proxy was not used in any further analyses of the timing of extreme events or regional compilation of events, although the large peaks at 550 and 150 Cal yr BP are briefly discussed later.

The correlation between water-table depth and humification at Saco Bog was $r = 0.55$ ($P < 0.01$), higher than at either Sidney Bog or Great Heath; however the detrended correlation was much lower ($r = 0.13$; not statistically significant at $\alpha = 0.05$), indicating the high correlation was driven by the long-term trends of both proxy records. Moisture

increased during the time period from 1800 Cal yr BP to 2300 Cal yr BP and high frequency variability recorded in both proxies between 1800 Cal yr BP and 2500 Cal yr BP, where four dry events were recorded in both proxy records (Figure 3.8). The charcoal record also shows a correspondence with inferred dry periods in both proxy records, with fire events occurring during dry periods at 550 Cal yr BP and 1450 Cal yr BP. During the 550 Cal yr BP period, both water-table depth and humification record a dry period, and multiple charcoal peaks occur at and around this time period including the peat fire associated with the hiatus in the record.

Stacked records and regional compilation of extreme wet and dry events

Each technique used to compile records revealed similar timings of wet and dry periods. For example, the driest time periods, based on magnitude, were centered at 550 Cal yr BP and 2300 Cal yr BP. The wettest periods occurred between 100 Cal yr BP and 460 Cal yr BP, with wettest pluvials centered between 2200 Cal yr BP and 2500 Cal yr BP. The time period between 1000 Cal yr BP and 1700 Cal yr BP was the least variable period in the record, recording the least amount of events (dry or wet) with a generally low probability of event occurrence. The highest probability of event occurrence (wet or dry) was during the past millennium.

Most extreme dry and wet events were recorded across all three sites, with seven distinct dry periods recorded by at least two sites and six distinct wet periods recorded by at least two sites (Table 3.1 and Table 3.2). However, eight distinct dry periods and nine distinct wet events occurred when only one site was recording an event, so that 100% of

inferred prolonged dry events and 67% of inferred prolonged wet events were recorded by at least two sites. Both dry and wet periods were centered on the time period of 1600 yr BP, which may be indicative of a highly dynamic time period (Figure 3.9 and Figure 3.10).

Comparison of all proxy records among sites shows coherent patterns of variability in wet and dry periods with the greatest confidence, or most amount of proxy record agreement (e.g., testate amoebae, humification, and charcoal), of widespread dry period centered at 550 Cal yr BP and the greatest confidence of wet periods centered at 460 Cal yr BP. At 550 Cal yr BP each site recorded a dry period from testate amoebae and humification proxies and each site recorded an upland fire. In fact, 550 Cal yr BP was the only time in the Great Heath and Saco Bog records where dry periods from both testate amoebae and humification proxies also corresponded with fire. Other dry periods with high agreement among proxies and sites occurred at 650 Cal yr BP and 800 Cal yr BP. At 800 Cal yr BP Sidney Bog and Great Heath recorded dry periods in both the humification and testate amoebae records, but neither recorded a fire. The hiatus at Saco Bog prevents comparison during this time. Interestingly, the time period between 400 Cal yr BP and 1000 Cal yr BP also had the highest number of extreme events (combined wet and dry events), and corresponds to the Medieval Climate Anomaly (MCA) and early-Little Ice Age (LIA). The wet events did not have as much coherence as dry events when comparing among sites or proxies. A wet period occurring at 460 Cal yr BP had the most proxy agreement among sites, when Saco Bog has a testate amoebae inferred wet period,

while both Sidney Bog and Great Heath recorded a wet period with water-table depth and humification.

Changes in the frequency of extreme events, both wet and dry, highlight how climate variability at multidecadal to multi-century timescales has changed over the past 3000 years. There were three time periods of increased extreme events, 400 to 1000 Cal yr BP, 1200 to 1500 Cal yr BP, and 2500 to 2200 Cal yr BP (Figure 3.10). A 400 year running sum of extreme events shows these patterns and highlights the increased extreme events that occurred from 400 to 1000 Cal yr BP, a time considered to comprise the MCA and the early portions of the LIA.

Discussion

Proxy record comparisons

Many studies have demonstrated the hydrological and climatic sensitivity of testate amoeba and humification records obtained from peatlands (e.g., Charman 2007; Booth et al. 2010; Amesbury et al. 2012). Hydrological sensitivity of peatland records can be assessed through comparison of hydrological proxies within the same core, and our testate amoeba and humification records showed considerable coherence within our three sites. However, as with any paleoclimatic archive, replication of wet and dry patterns at multiple sites within the same region, and/or comparison of upland and peatland proxies from within the same core (e.g., Clifford and Booth 2013, 2015), provide support for climatic interpretations of hydrological changes. In our three records from Maine, microscope charcoal spikes derived from regional fires are centered on time

periods when paleohydrological proxies indicate dry periods, and several major times of dry periods were replicated across multiple sites, providing confidence in the climatic interpretation of the extreme events in our reconstructions (i.e., Booth et al. 2003; Hughes et al. 2006; Swindles et al. 2013).

The strengths of testate amoeba-based water-table depth reconstructions include the robust relationship between many amoebae taxa and water-table depth and the universal finding that surface-moisture is the primary control on testate amoeba community composition in oligotrophic peatlands worldwide (Charman 2001; Booth 2002; Wilmshurst et al. 2003; Booth 2008; Van Bellen et al. 2014). However, cautious interpretation of fossil assemblages containing taxa with little modern representation in regional calibration sets, such as *Difflugia pristis* type in this study, is warranted. Although *D. pristis* was present in all of our records, it was rarely present during the extreme events identified in this study, and when the taxa were present it was a minor (< 5%) component of the testate amoebae community. While several taxa unrepresented in modern samples were found at each site, the majority of taxa during inferred wet periods (e.g., *A. flavum, A. discoides*, etc.) and dry periods (e.g., *T. arcula*, *T. minuta*, *H. subflava*, etc.) have very well characterized hydrological niches (i.e., Booth 2002, Booth 2008), improving confidence in the transfer function (Payne et al. 2016).

Measurements of peat humification have a long history in peatland studies, and quantitative assessments are commonly utilized as a quick and relatively inexpensive hydroclimate proxy; however, other environmental factors also effect peat humification, particularly the botanical composition of the peat (Yeloff and Mauquay 2006; Hughes et

al. 2012). Often, humification analysis is co-conducted with testate amoebae analysis to provide an independent test of both proxy records (Hughes et al. 2006), which was done here with a generally statistically significant correlation between the two proxy records. Utilizing humification as a validation for water-table depth worked well at these sites and provided additional confirmation of extreme events, however there were time periods at each site when the two proxy records did not correlate well, indicating caution should be used during validation. Furthermore, the potential for secondary decomposition in peatlands provides an added complexity in the interpretation (i.e., Morris et al. 2015).

Unlike the good correspondence between humification and testate amoebae observed in the three records in this study, the SVR proxy did not correlate well with either humification or water-table depth reconstructions at Great Heath, the one site where it was applied. The reasons for the poor correlation between humification/water-table depth and SVR are not fully understood, as the SVR uses the relative abundance of n-alkanes to infer relative changes in *Sphagnum* and vascular plants (Nichols et al. 2006; Nichols and Huang 2007). Often the ratio is interpreted as reflecting the relative abundance of ericaceous shrubs, which would be expected to expand at the expense of *Sphagnum* during drier time periods. However, an expansion of sedges could also produce a shift in the SVR record, and such complexities complicate interpretation of the proxy. The SVR record did, however, record dry events, or decreased *Sphagnum* relative to vascular plants, at 550 Cal yr BP and 150 Cal yr BP, suggesting that while SVR was not well correlated overall to the other proxies, the dry event at 550 Cal yr BP observed at all sites and virtually all proxies, was recorded in the SVR record. The SVR record also

showed decreased abundance of *Sphagnum* (interpreted as a dry climate) at 150 Cal yr BP, which was near the peak of European land-clearance, and land-use changes drove many vegetation changes on peatlands in the Northeast, often resulting in decreased *Sphagnum* (Ireland et al. 2014). Given the reliance of the SVR proxy on the plant composition, SVR may more appropriately be interpreted if conducted alongside plant macrofossil analysis to provide botanical context.

Stacked records – site comparisons

The stacked records identified several time periods of extreme wet and dry phases, which were recorded in the peatland records. Two of the three most severe dry periods of the past 3000 years occurred in the past millennia at 550 Cal yr BP and 800 Cal yr BP, while other prolonged dry periods were centered on 1600 Cal yr BP and 2300 Cal yr BP (Table 3.1; Figure 3.10A, 3.10B). The dry period occurring at 2300 Cal yr BP was also observed in lake-level studies in the region (Shuman et al. 2001; Newby et al. 2014). The 550 Cal yr BP dry period was recorded in all proxy records at all three sites, was associated with fires at all sites, and has also been directly linked with widespread upland forest community change (Clifford and Booth 2015). Also, dry periods at 650 Cal yr BP and 1100 Cal yr BP were recorded in nearly all proxy records. When records were compared among sites, all records of extreme dry events were coherently recorded between at least two sites, but only 67% of wet periods were synchronously recorded. Wet events were recorded with much less coherence among proxy records and sites, suggesting both humification and testate amoeba may be better at recording dry time

periods rather than wet time periods, consistent with past interpretations in North America (i.e., Booth et al. 2005; Booth et al. 2006; Clifford and Booth 2015) and recent modeling studies (Morris et al. 2015). Additionally, there was no coherent pattern to explain why one site recorded an event and another site did not. For example, site location such as northern Maine or southern Maine – or coastal Maine and inland Maine did not explain patterns of disagreement among sites. An explanation for the disagreement in patterns among sites may be due to autogenic processes.

The continuous stacked records and the event-based probability stacked record were in good agreement for most inferred extreme events. Although some events do not show similar magnitudes (i.e., dry period at 650 Cal yr BP; Figure 10), which is likely because the continuous stacked records were derived from the best-fit line of the age-depth model (i.e., a single data point for each site at each time) which drives the timing of the continuous stacked records, whereas the event-based stacked records use the probability distribution. Additionally, in the event-based stacked records, there was "smearing" of events, due to the wide range of age uncertainty (Figure 9; Figure 10F). However, the "age-smearing" provides a conservative estimation of the timing of an event and may capture more than one event, which was likely the case for the wet periods at 1600 and 1700 Cal yr BP (Figure 9).

Late-Holocene fires in Maine occurred significantly more frequently during dry events than during average hydroclimate conditions or wet periods (Clifford and Booth 2013), although fires were rarely recorded synchronously between the three peatlands sites. The only time when fires were synchronous was at 550 Cal yr BP, which is also the

time period when regional forest composition rapidly shift (i.e., Fuller et al. 1998; Clifford and Booth 2015). However, other fires throughout the record were associated with dry events or were recorded simultaneously by either proxy records among sites. For example, both Sidney Bog and Saco Bog indicate fire during dry periods recorded in humification and water-table depth proxy records from 2200 to 2300 Cal yr BP. Additionally, at ~1100 Cal yr BP both proxy records in Sidney Bog recorded a dry period, while fire was also indicated. However, only Sidney Bog has a record during that time as Saco Bog had a hiatus and the Great Heath proxy records do not extend that far. Both time periods occur when lake records in the region also record dry periods (Li et al. 2007; Newby et al. 2014).

Regional climate patterns

Regional climate records indicate the past 3000 years was relatively wet compared to the early and mid-Holocene (Shuman et al. 2001; Hubeny et al. 2015). However, our results show the past 3000 years have been punctuated by several prolonged dry periods and the hydroclimate of the Northeast was highly variable at decadal-to-multidecadal scales. These prolonged dry periods of the past 3000 years have also been shown by others (i.e., Shuman et al. 2009; Pederson et al. 2013; Newby et al. 2014), or eluded to in the form of paleoecological reconstructions (i.e., Fuller et al. 1998; Paquette and Gajewski 2013). Lake-level reconstructions from northeastern North America indicate a generally dry period occurred between 2100 and 2900 yr BP and between 1200 and 1300 Cal yr BP (Li et al. 2007; Newby et al. 2014), both time periods

that correspond within the uncertainty of the age models to dry periods in the peatland record (Figure 3.10). Our records also correspond to previously identified wet periods of 2600 Cal yr BP (Brown et al. 2000) and 430 Cal yr BP (Pederson et al. 2013; Figure 3.10F). Furthermore, our records also support the notion that the MCA in eastern North America was a hydroclimatically variable time period with pronounced dry events (Cook et al. 2004; Booth et al. 2006; Booth et al. 2012). Our records show that the past millennium was particularly variable compared to the previous two millennia. The most severe dry period that occurred in our records was the 550 Cal yr BP dry period that had major impacts on the ecosystems of the region, indicated by a rapid change in forest taxa (Fuller et al. 1998; Paquette and Gajewski 2013; Clifford and Booth 2015). However, our records also record dry periods at 650 Cal yr BP and 800 Cal yr BP – a similar pattern, albeit different in timing than three prolonged MCA droughts recorded in the Great Lakes and western North America (i.e., Cook et al. 2004; Booth et al. 2006). Comparisons of decadal-to-multidecadal scale peatland records, such as the ones presented here, to the millennial scale records such as those from lake-level studies, are difficult because of different sensitivities, time-integration, and resolution. Lake-level studies have revealed millennial-scale changes in the moisture balance of the Northeast, but linking dry periods from these studies to those found in peatland studies has been difficult.

Utilizing multiple stacked records

I examined the late-Holocene hydroclimate variability in the northeastern North America by developing several new methods of stacking hydroclimate records from

peatlands, with a focus on the identification of extreme events. Most previous work has focused on developing continuous timeseries of hydroclimatic changes from multiple records (e.g., Charman et al. 2006; Swindles et al. 2013), although there is considerable interest in extreme events as drivers of ecosystem changes. In this study, I examined four different methods of presenting and analyzing records from multiple proxies, by using the method of Charman et al. (2006), a weighted stacking method, a compilation of testate amoebae, humification, and charcoal, and a probabilistic method of extreme event compilation (Figure 3.10).

I developed multiple stacked records to compare the paleohydrology in northeastern North America. Each stacked record has advantages and disadvantages and all are more appropriately used together. The Charman et al. (2006) method of record stacking, as well as the weighted stacking method, highlight the magnitude of events and show the dry period at 550 Cal yr BP and 2300 Cal yr BP were the two driest time period in the record. Combining the Charman et al. (2006) method with the weighted stacking method allowed for increased emphasis to be placed on time periods with high agreement with the humification record, and not just water-table depth reconstructions. The running sum of events (Figure 3.10C) provided insights into temporal variability of event occurrence. For example, this method of record stacking identified the increased variability during the time period of 400 to 1000 Cal yr BP relative to other time periods. The probability of event occurrence provided an estimated time-range of events (e.g., the dry period centered at 800 Cal yr BP ranged between 730 Cal yr BP and 930 Cal yr BP). Additionally, the events with the highest probability of occurrence were the wet period

that occurred at 120 Cal yr BP and the dry period that occurred at 650 yr BP. Using multiple proxy-climate records along with multiple methods to compile records provides a clearer understanding of the magnitude of extreme events, the variability of the records, and the timing of events.

Value of composite climate record

Insights from multiproxy – multisite compilations and analyses provide increased robustness of paleohydrological records. And further, the multidecadal nature of the peatland archive provides an ideal time resolution to fill the gap between annually resolved tree-ring studies, annually resolved varved lake sediment studies, and the centennial-to-millennial scale lake-level studies. An additional advantage of using a multisite design is the regionality provided, which has an increased usefulness in testing regional climate models. However, a next step in integrating climate records is the compilation of lake, peatland (i.e., Barber et al. 2013), and tree-ring records – and the development of techniques to integrate results from these climate recording archives on different time-scales and frequencies. The integration of multiple sites over large spatial areas can provide a clearer understanding of the conditions that drive prolonged extreme events (i.e., Cook et al. 2004; Cook et al. 2010; Swindles et al. 2013). The stacked record provides evidence that the late Holocene hydroclimate was highly variable, with seven prolonged dry periods and six prolonged wet periods (Figure 3.10). While such records provide evidence of past hydrological variability, and in this case of a highly populated region of northeastern North America. Future models predict northeastern North America

will continue to increase in average precipitation (Collins et al. 2013), much as it has during the past 3000 years (Shuman et al. 2001; Hubeny et al. 2015). However, records such as those presented here highlight the potential for prolonged dry and periods to occur during such long-term, millennial-scale “wet periods” (i.e., long-term average increase in precipitation, but punctuated with extreme dry/wet periods), and such decadal-to-multidecadal droughts have triggered widespread changes to disturbance regimes and forest composition in the recent past. As human-induced climate change accelerates the rate of change, punctuated wet and dry periods have the potential to add tremendous economic cost to the region from direct impacts (i.e., flooding) and indirect impacts (i.e., loss of ecosystem services).

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Table 3.1. Age of dry periods recorded at each peatland. The same letter in timing indicates the event was the same among sites.

Site	Mean age (Cal yr BP)	Lower age range (Cal yr BP)	Upper age range (Cal yr BP)	Event	Proxy	Timing
Saco Bog	-40	-60	60	Dry	Testate	a
Great Heath	-10	-50	160	Dry	Testate	a
Sidney Bog	120	70	230	Dry	Testate	
Great Heath	160	108	320	Dry	Testate+CHAR	b
Sidney Bog	190	130	270	Dry	Testate	b
Sidney Bog	300	210	390	Dry	Testate+Humification	c
Great Heath	310	280	490	Dry	Testate+Humification	c
Saco Bog	360	290	400	Dry	Testate	c
Saco Bog	470	410	510	Dry	Testate	d
Saco Bog	490	460	530	Dry	All	d
Saco Bog	530	500	550	Dry	All	e
Sidney Bog	560	540	700	Dry	All	e
Great Heath	580	510	670	Dry	All	e
Saco Bog	580	530	620	Dry	Testate+CHAR	e
Great Heath	650	640	690	Dry	Testate	
Great Heath	800	740	830	Dry	Testate+Humification	f
Great Heath	820	770	860	Dry	Testate+Humification	f
Sidney Bog	840	740	880	Dry	Testate+Humification	f
Great Heath	860	790	910	Dry	Testate	f
Sidney Bog	900	800	920	Dry	Testate	f
Sidney Bog	1070	990	1170	Dry	Testate+Humification	
Sidney Bog	1120	1060	1190	Dry	All	
Sidney Bog	1260	1160	1290	Dry	Testate	
Sidney Bog	1290	1180	1430	Dry	All	
Sidney Bog	1420	1390	1550	Dry	All	g
Saco Bog	1470	1100	1530	Dry	Testate+CHAR	g
Saco Bog	1580	1460	1640	Dry	Testate	
Sidney Bog	1640	1510	1760	Dry	Testate+Humification	h
Sidney Bog	1700	1570	1810	Dry	Testate+Humification	h
Sidney Bog	1850	1680	2110	Dry	Testate+CHAR	i
Saco Bog	1860	1660	1870	Dry	Testate	i
Saco Bog	1890	1740	1950	Dry	Testate	i
Sidney Bog	2080	1980	2770	Dry	Testate+Humification	j
Saco Bog	2120	2060	2200	Dry	Testate	j
Saco Bog	2150	2080	2230	Dry	Testate+Humification	
Saco Bog	2300	2230	2360	Dry	Testate+Humification	k
Sidney Bog	2320	2070	2830	Dry	Testate	k
Saco Bog	2360	2300	2400	Dry	Testate+Humification	k
Saco Bog	2450	2340	2490	Dry	Testate+Humification	
Saco Bog	2460	2390	2520	Dry	Testate	
Sidney Bog	2700	2120	3000	Dry	Testate+CHAR	

Table 3.2. Age of wet periods recorded at each site. The same letter in timing indicates the event was the same among sites.

Site	Mean age (Cal yr BP)	Lower age range (Cal yr BP)	Upper age range (Cal yr BP)	Event	Proxy	Timing
Sidney Bog	-50	-270	170	Wet	Testate+humification	
Sidney Bog	50	20	220	Wet	Testate	a
Saco Bog	100	30	130	Wet	Testate	a
Saco Bog	130	80	150	Wet	Testate	
Saco Bog	140	100	160	Wet	Testate	
Saco Bog	180	160	200	Wet	Testate	
Sidney Bog	340	230	450	Wet	Testate+humification	b
Great Heath	390	340	510	Wet	Testate	b
Saco Bog	420	320	460	Wet	Testate	b
Saco Bog	450	370	490	Wet	Testate	
Saco Bog	460	380	500	Wet	Testate	c
Sidney Bog	470	370	610	Wet	Testate	c
Sidney Bog	510	430	670	Wet	Testate	d
Great Heath	530	490	630	Wet	Testate+humification	d
Great Heath	800	740	820	Wet	Testate+humification	
Great Heath	820	770	850	Wet	Testate+humification	
Great Heath	890	790	950	Wet	Testate	
Great Heath	930	820	970	Wet	Testate	
Sidney Bog	950	850	1020	Wet	Testate	
Sidney Bog	1000	920	1120	Wet	Testate	
Sidney Bog	1250	1130	1380	Wet	Testate+humification	
Saco Bog	1340	1000	1516	Wet	Testate	e
Sidney Bog	1350	1250	1490	Wet	Testate	e
Saco Bog	1390	1240	1570	Wet	Testate	e
Sidney Bog	1490	1430	1630	Wet	Testate+humification	f
Saco Bog	1550	1450	1620	Wet	Testate	f
Saco Bog	1610	1510	1740	Wet	Testate	
Sidney Bog	1760	1620	1880	Wet	Testate	g
Saco Bog	1780	1600	1850	Wet	Testate	g
Sidney Bog	1800	1630	1930	Wet	Testate	
Sidney Bog	1890	1710	2200	Wet	Testate	
Sidney Bog	1940	1740	2240	Wet	Testate	
Sidney Bog	1970	1800	2270	Wet	Testate	h
Saco Bog	1980	1840	2010	Wet	Testate	h
Saco Bog	2000	1900	2020	Wet	Testate	
Saco Bog	2010	1920	2030	Wet	Testate	
Saco Bog	2020	1930	2060	Wet	Testate	
Saco Bog	2210	2140	2310	Wet	Testate+humification	
Saco Bog	2230	2180	2320	Wet	Testate+humification	
Saco Bog	2240	2190	2330	Wet	Testate+humification	
Saco Bog	2260	2210	2350	Wet	Testate	
Saco Bog	2460	2400	2530	Wet	Testate	
Saco Bog	2480	2410	2540	Wet	Testate	
Saco Bog	2500	2410	2590	Wet	Testate	

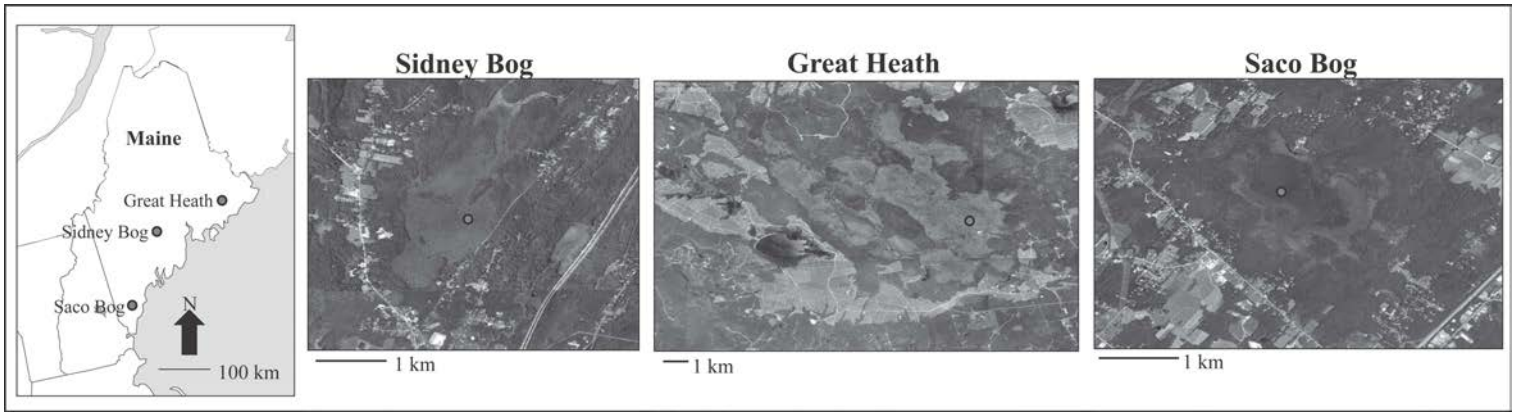

Figure 3.1. Regional location of each peatland. Aerial photos show the peatlans and dots mark the coring location.

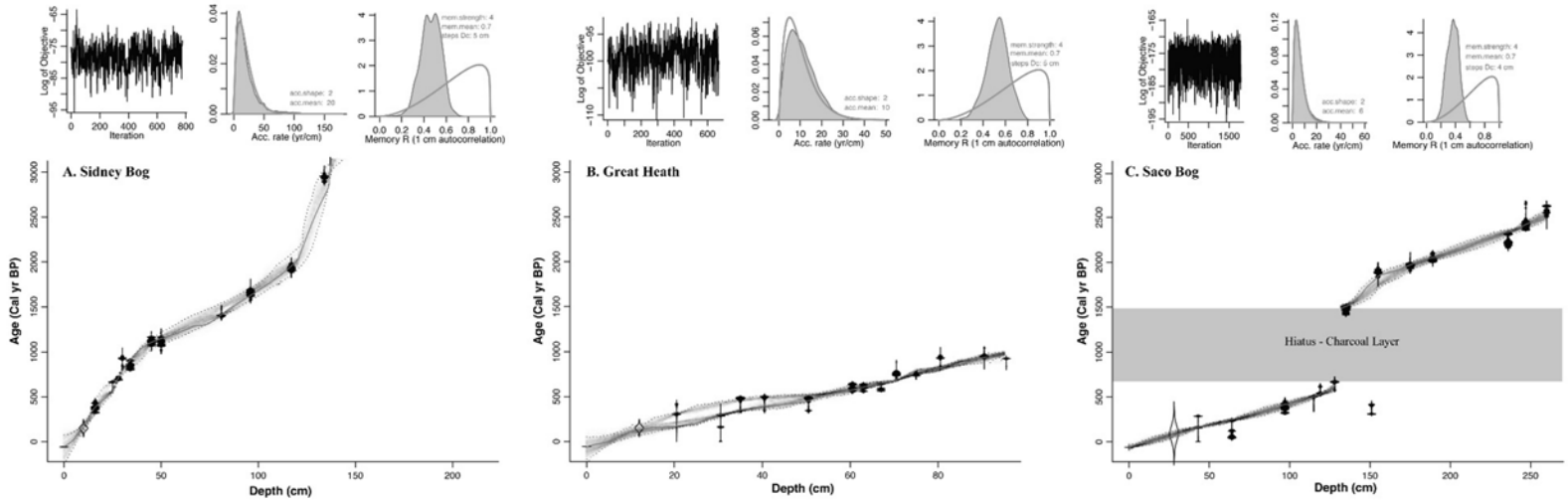

Figure 3.2. Age-depth models from Sidney Bog (left), Great Heath (middle), and Saco Bog (right). Top graphs are the prior distributions used to develop age-depth models (Blaauw and Christen 2011). Lower graphs show the age-depth models for each site. The black probability density dots show the probability distribution of the calibrated ^{14}C dates. The gray shaded region is a 95% envelope, with darker gray shading occurring in regions with higher probability density. Solid line represents the best fit line (Figure from Clifford and Booth 2013).

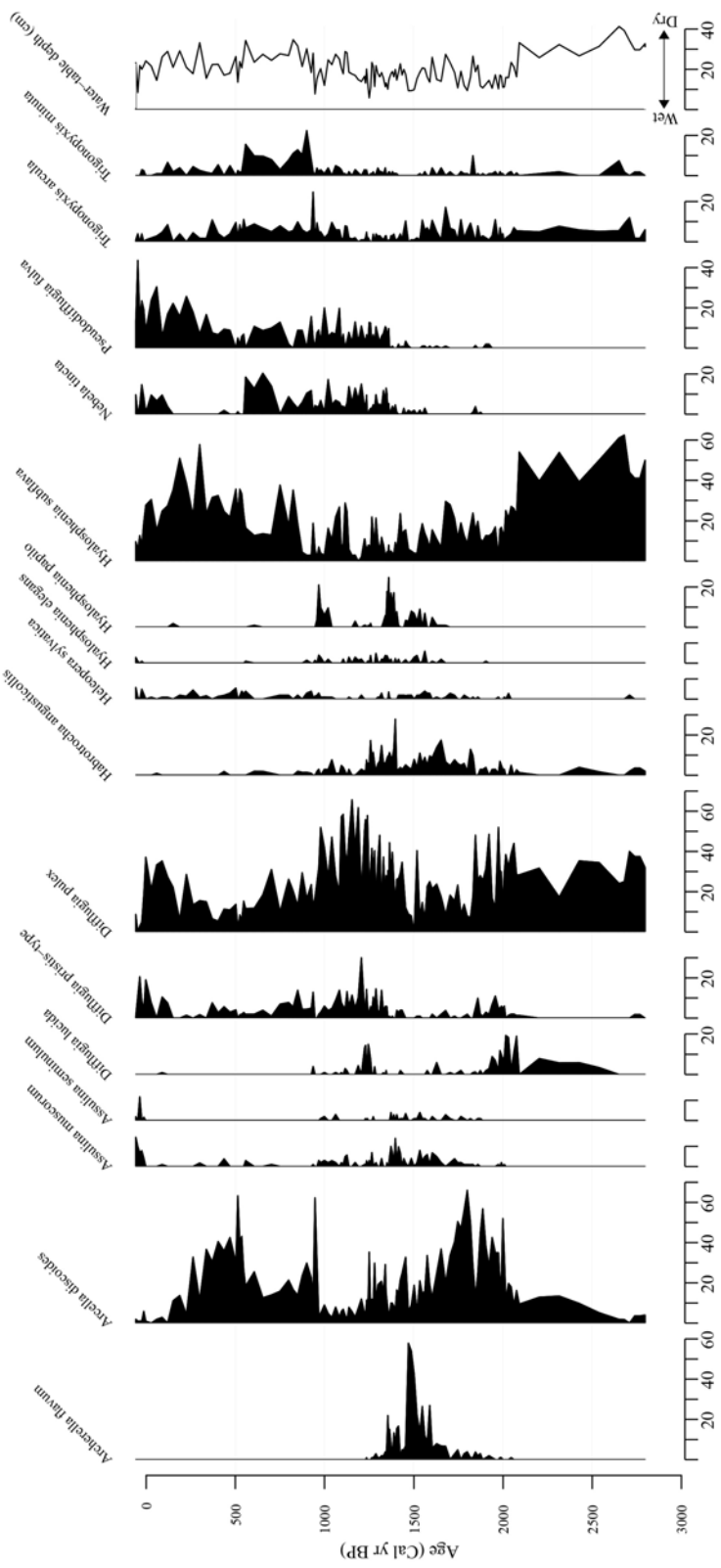

Figure 3.3. Stratigraphic community composition of testate amoebae from Sidney Bog. (Figure modified from Clifford and Booth 2013)

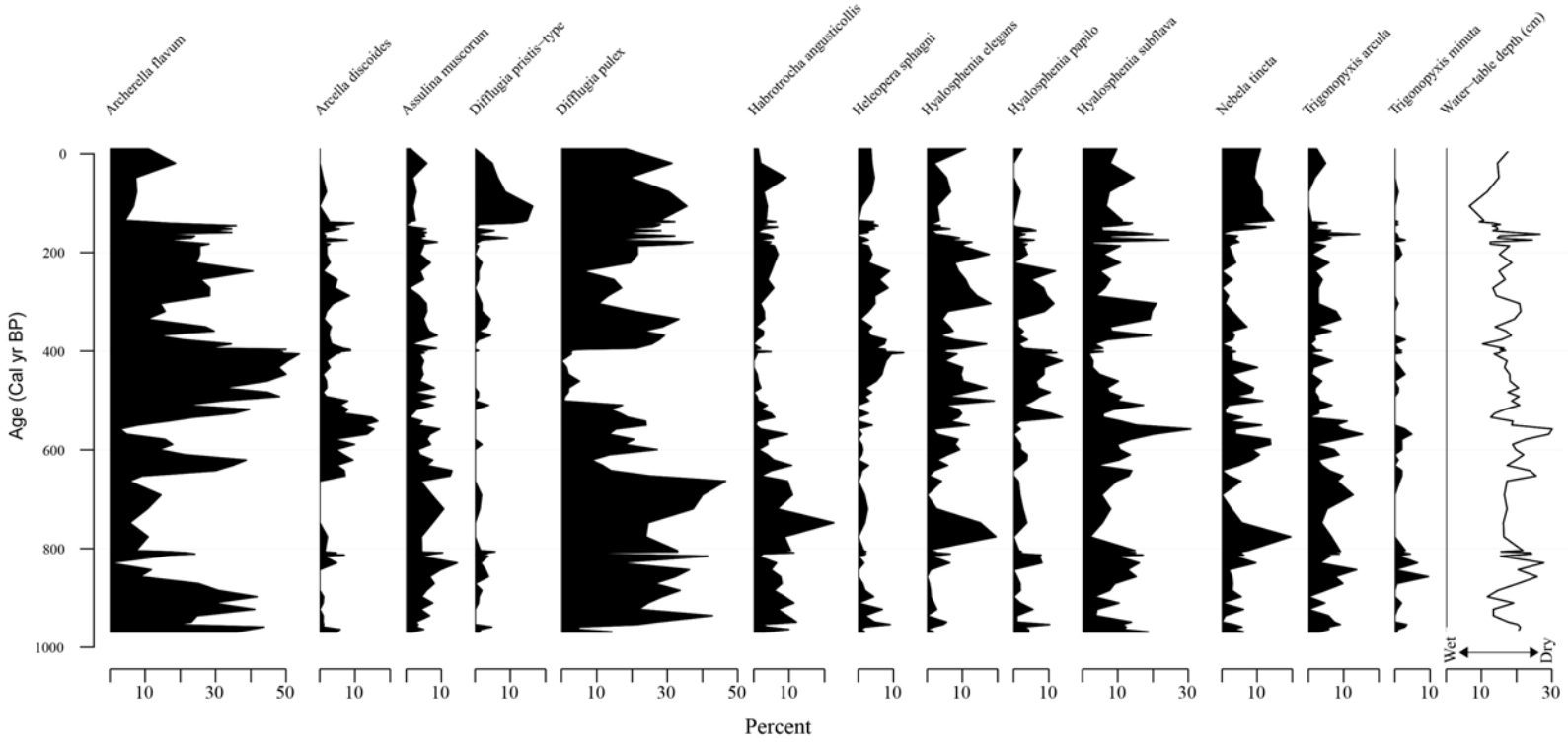

Figure 3.4. Stratigraphic community composition of testate amoebae from Great Heath. (Figure modified from Clifford and Booth 2013).

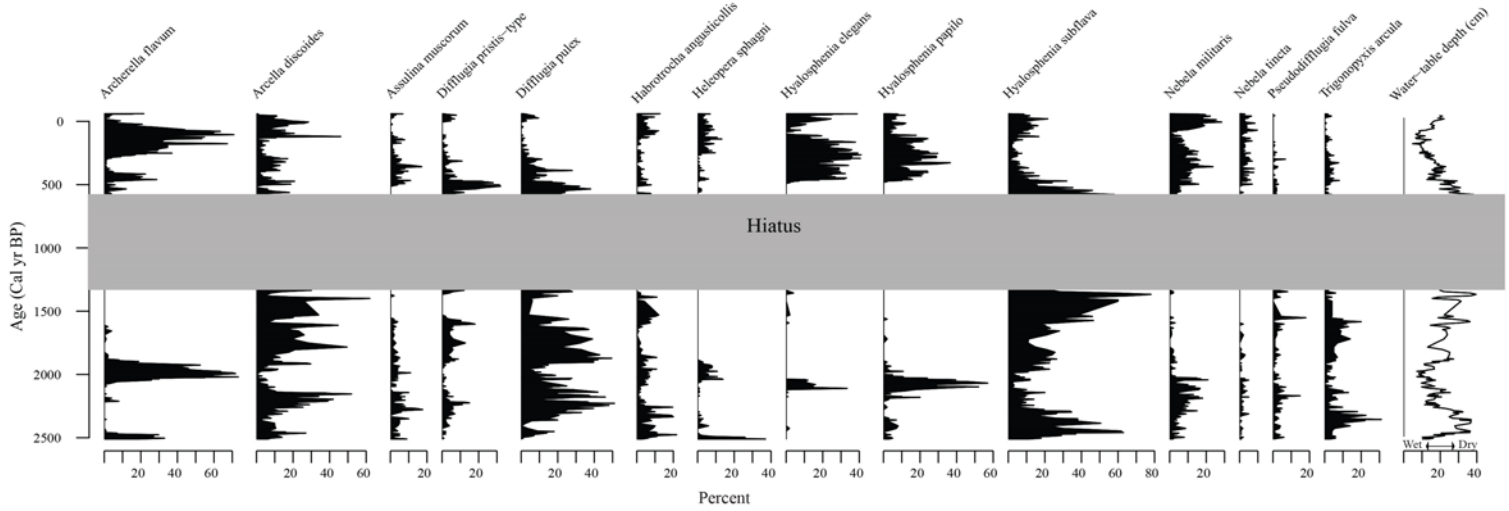

Figure 3.5. Stratigraphic community composition of testate amoebae from Saco Bog. Figure modified from Clifford and Booth 2013).

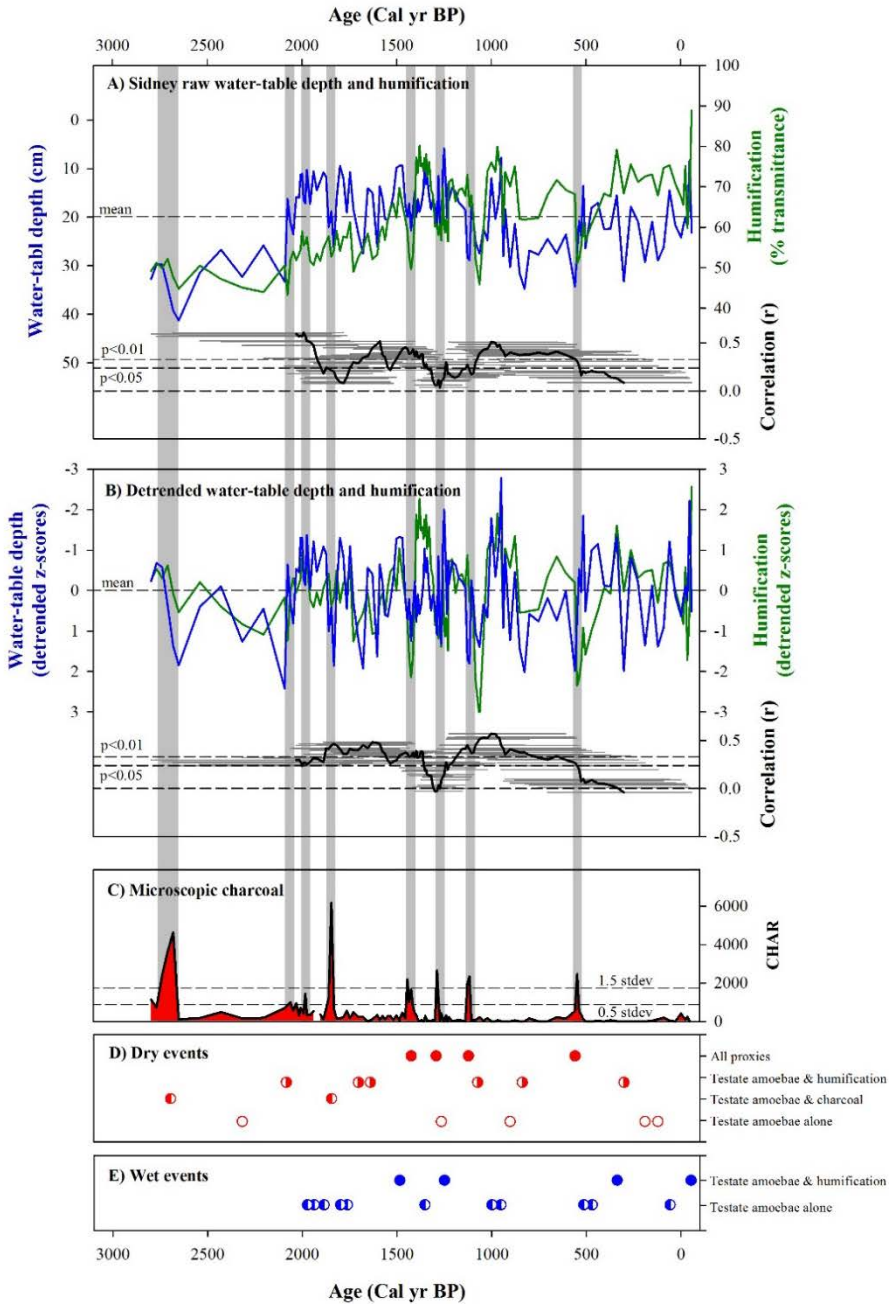

Figure 3.6. A) Raw water-table depth and humification records with the corresponding running correlations at Sidney Bog. B) Detrended proxy water-table depth and humification records with the corresponding running correlation, with gray bars indicating the samples used for each running correlation value. C) Microscopic charcoal records from Sidney Bog. D) Mean age of drought events among proxy records. E) Mean age of pluvial events among proxy records.

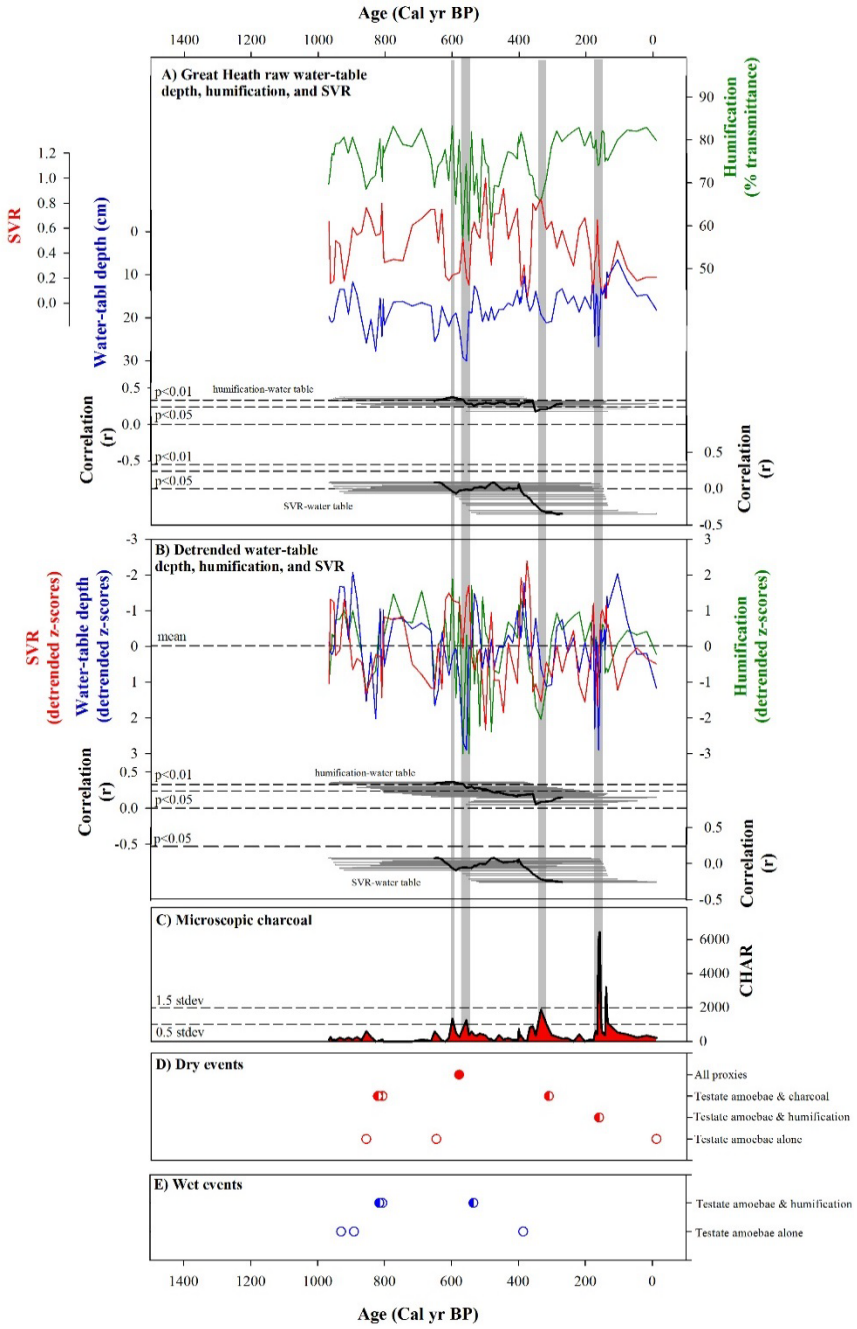

Figure 3.7. A) Raw hydroclimate proxy records (water-table depth, humification, and SVR) with the corresponding running correlations to water-table depth at Great Heath. B) Detrended proxy hydroclimate records (water-table depth, humification, and SVR) with the correlations to water-table depth. C) CHAR record from Great Heath. D) Mean age of dry events among proxy records. E) Mean age of pluvial events among proxy records.

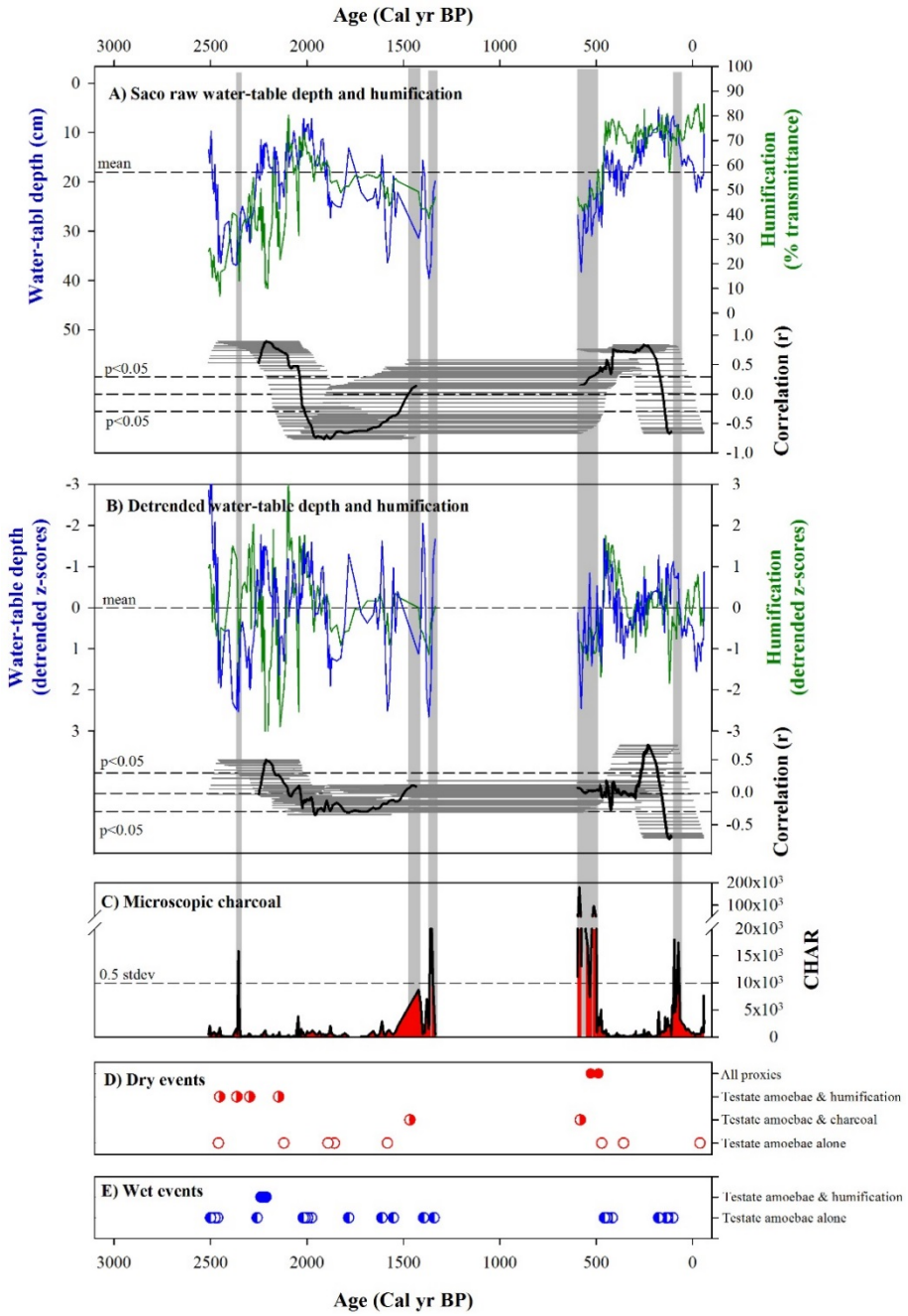

Figure 3.8. A) Raw water-table depth and humification records with the corresponding running correlations at Saco Bog. B) Detrended proxy water-table depth and humification records with the corresponding running correlation. C) Microscopic charcoal records from Saco Bog. D) Mean age of dry events among proxy records. E) Mean age of pluvial events among proxy records.

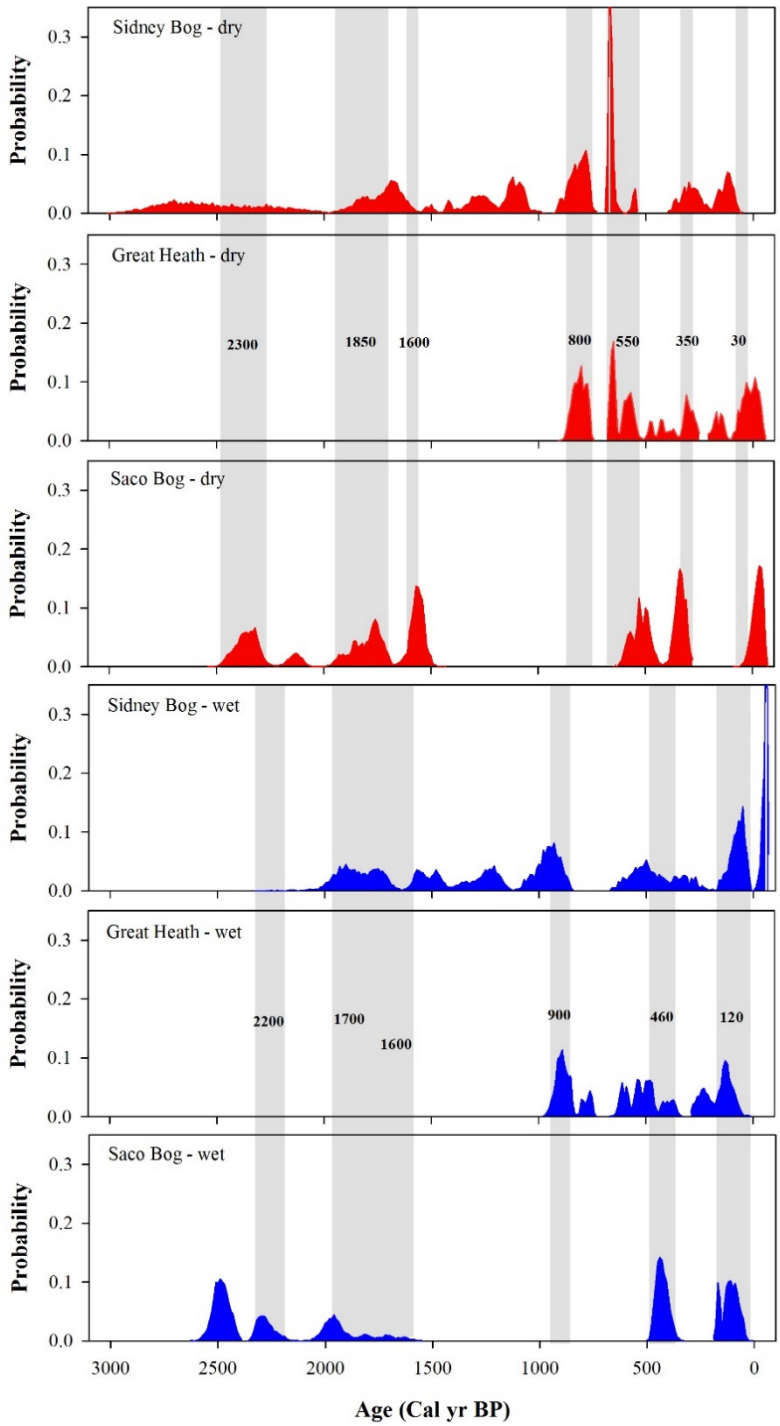

Figure 3.9. The probability of dry event (top three panels) occurrence at each site. Wet period probability occurrences are shown on the bottom three panels. Ages (Cal yr BP) shown on the Great Heath panels correspond to synchronous wet/dry periods.

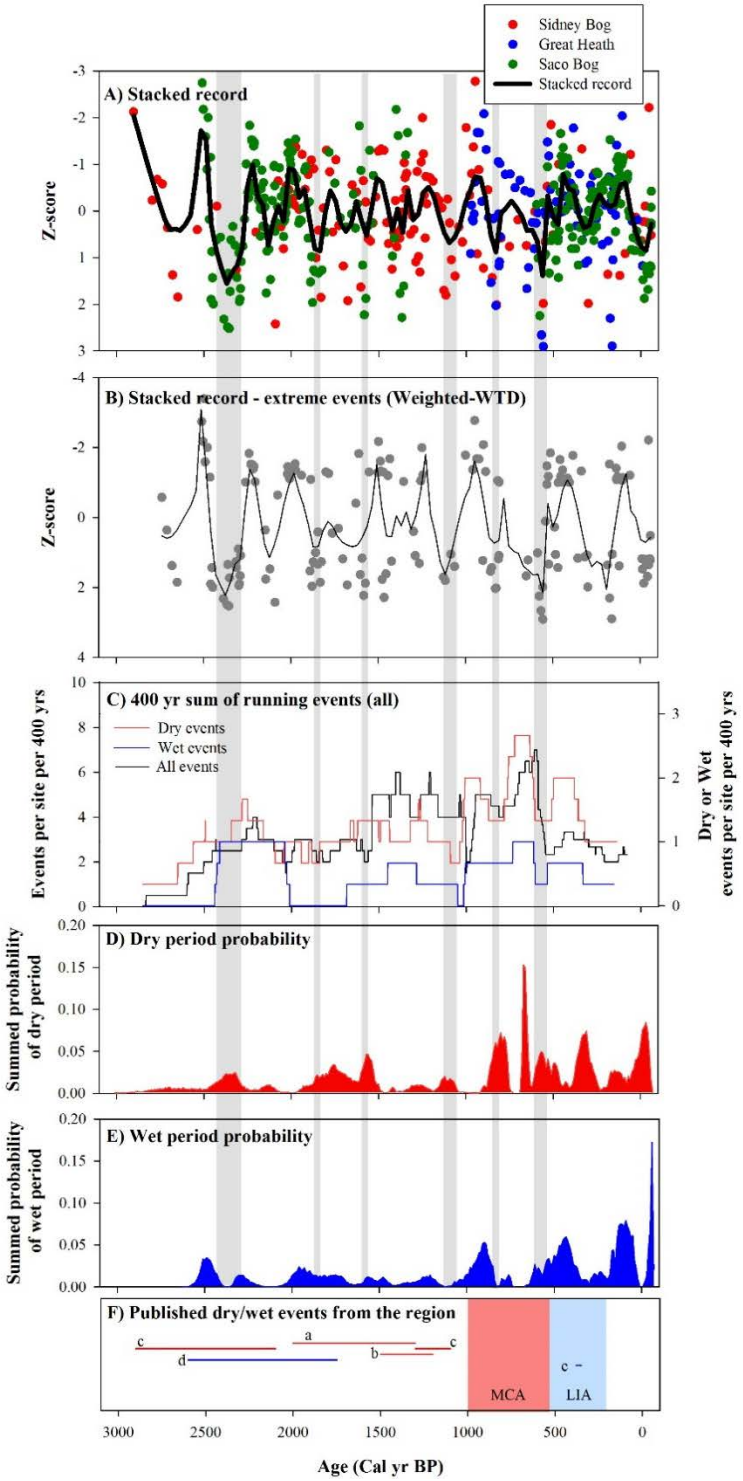

Figure 3.10. A) The stacked record (Charman method), with each site shown as a different color. B) Stacked record weighted based on number of climate proxy agreements (i.e., more agreements

within a site was weighted more heavily). C) A 400 running count of dry events (red line), pluvial events (blue line), and total extreme events (black line). D) Compiled probability of dry occurrences among all sites. E) Compiled probability of pluvial occurrences among all sites. F) Regional dry/wet periods from published literature in the region (citations below), MCA (Medieval Climate Anomaly), and LIA (Little Ice Age).

a) Dry: Hubeny et al. (2015)

b) Dry: Li et al. (2007)

c) Dry: Newby et al. (2014)

d) Wet: Brown et al. (2000)

e) Wet: Pederson et al. (2013)

Conclusions

This research presented in this dissertation has contributed to a better understanding of the long-term linkages between hydroclimate, fire, and vegetation change during the late Holocene of the Northeastern USA. During the past 3000 years, the climate of the Northeast has been characterized by several prolonged and severe droughts and these dry periods significantly increased the probability of fire occurrence in the region, and the most severe of these droughts clearly lead to a rapid shift in forest composition about 550 years ago. Interestingly, forest composition was permanently altered by this multidecadal spanning drought event and the associated fires, and these changes persisted until European settlement. While historical records of the past century suggest a relatively moist climate and low fire landscape – my work highlights that considerably more variability occurred in the past, and management and adaptation plans under future projected climate change need to consider the potential for widespread decadal-spanning drought and altered fire regimes in the future.

Results from Chapter 1 showed that fire occurrence was significantly higher during drought periods, compared to average conditions or pluvial periods. However, while drought significantly increased the probability of fire occurrence at each site, the three peatlands only recorded fires synchronously one time during the 3000 year record, which was 550 Cal yr BP. The lack of synchronous fires indicated that fires were often spatially heterogeneous, yet probabilistically linked to climate variability at each site, during the late Holocene.

Results from Chapter 2 indicated that over 70% of sites underwent a significant change in forest composition after the drought and fires of 550 Cal yr BP. The transition was characterized by a change from abundant beech (*Fagus grandifolia*) and hemlock (*Tsuga canadensis*) to greater representation by pines (*Pinus* spp.) and oaks (*Quercus* spp.). High resolution analysis of the pollen record from Sidney Bog and Saco Bog shows that each peatland recorded drought and fire, and that vegetation shifts were lagged by about one to two decades, consistent with post-fire recovery. Why the changes in response to this transient drought event persisted until European settlement remains unresolved; however, the change occur prior to climatic cooling from the Little Ice Age, with post-fire succession likely playing out against the low-frequency temperature trends of this time period.

The results from Chapter 3 showed that Northeast hydroclimate was highly variable during the past 3000 years, with at least eight prolonged dry events and nine prolonged wet events. Dry events were recorded synchronously among all sites, but only 67% of wet periods were recorded synchronously among sites, suggesting peatland hydroclimate proxies may record dry periods better than wet periods. I developed several new methods for examining and hydroclimate records from multiple peatland sites. Future efforts toward combining the records from multiple paleoclimate archives (e.g., bogs, lakes, tree-rings) would potentially significantly improve our understanding of climate variability at frequencies ranging from millennial to interannual.

Vita

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Education

2008 M.S. Biology, Northern Arizona University
2005 B.S. Biology, Westminster College

Employment & Appointments

2014-present Assistant Research Scientist, Range Ecology, Desert Research Institute
2010-present Affiliate, Merriam-Powell Center for Environmental Research
2010-2014 Graduate Research/Teaching Assistant, Lehigh University
2005-2009 Ecologist, Merriam-Powell Center for Environmental Research
2005-2008 Graduate Assistant, Department of Biology, Northern Arizona University
2003-2005 Plant Research Technician, Department of Biology, Westminster College

Publications

Peer-Reviewed

Redmond, M.D., N.S. Cobb, M.J. Clifford, and N.N. Barger. 2015. Woodland recovery following drought-induced tree mortality across an environmental stress gradient. Global Change Biology, doi: 10.1111/gcb.12976

Clifford, M.J. and R.K. Booth. 2015. Late-Holocene drought and fire drove a widespread change in forest community composition in eastern North America. The Holocene 25:1102-1110.

Ireland, A.W., **M.J. Clifford**, and R.K. Booth. 2014. Widespread dust deposition on North American peatlands coincident with European land-clearance. Vegetation History and Archaeobotany 23:693-700.

Delph, R.J., **M.J. Clifford**, N.S. Cobb, P.L. Ford, and S.L. Brantley. 2014. Pinyon pine mortality alters ground-dwelling arthropod communities. Western North American Naturalist 72:162-184.

Clifford, M.J., P.D. Royer, N.S. Cobb, D.D. Breshears, and P.L. Ford. 2013. Precipitation thresholds and drought-induced tree die-off: insights from patterns of *Pinus edulis* mortality along an environmental stress gradient. New Phytologist 200:413-421, doi: 10.1111/nph.12362.

Clifford, M.J. and R.K. Booth. 2013. Increased probability of fire during late Holocene droughts in northern New England. Climatic Change 119:693-704, doi:10.1007/s10584-013-0771-y.

Booth, R.K., S.T. Jackson, V.A. Sousa, M.E. Sullivan, T.A. Minckley, and **M.J. Clifford**. 2012. Multidecadal drought and amplified moisture variability drove rapid forest community change in a humid region. Ecology 93:219-226.

Lindsay, D.L., P. Bailey, R.F. Lance, **M.J. Clifford**, R. Delph, and N.S. Cobb. 2011. Effects of a nonnative, invasive lovegrass on *Agave palmeri* distribution, abundance, and insect pollinator communities. Biodiversity and Conservation 20:3251-3266 doi:10.1007/s10531-011-0133-x.

Clifford, M.J., N.S. Cobb, and M. Buenemann. 2011. Long-term tree cover dynamics in a pinyon-juniper woodland: drought resets successional clock. Ecosystems 14:949-962 doi:10.1007/s10021-011-9458-2.

Royer, P., N.S. Cobb, **M.J. Clifford**, C. Haung, D.D. Breshears, H.D. Adams, and J.C. Villegas. 2011. Extreme climatic event-triggered overstorey vegetation loss increases understorey solar input regionally: primary and secondary ecological implications. Journal of Ecology 99:714-723.

Floyd, M.L., **M. Clifford**, N. Cobb, D. Hanna, R. Delph, P. Ford, and D. Turner. 2009. Relationship of stand characteristics to drought-induced mortality in piñon-juniper woodlands in Colorado, Arizona and New Mexico. Ecological Applications 19:1223-1230.

Technical Reports

Clifford, M.J. 2016. Biological Report for the Fiber Optic Line between P-56 and Station 80 on the Tonopah Test Range, Nevada. DRI Biological Report No. BA091014-1.

Clifford, M.J. 2016. Literature Review of Ecological Restoration Techniques Specific to CAU 111 at the Area 5 Radioactive Waste Management Compound at the Nevada National Security Site. DOE/NV-In press. Las Vegas, NV.

Clifford, M.J. 2015. Biological Report for the Sandia Fiber Optic Line on the Tonopah Test Range. DRI Biological Report No. BA062915-1.

Lindsay, D.L., P. Bailey, R.F. Lance, **M.J. Clifford**, R. Delph, and N.S. Cobb. 2010. Effects of a nonnative, invasive lovegrass on *Agave* distribution, abundance, and pollinator community composition. ERDC/EL-TN-10-1.

Clifford, M.J., M.E. Rocca, R. Delph, P.L. Ford, and N.S. Cobb. 2008. Drought induced tree mortality and ensuing bark beetle outbreaks in Southwestern pinyon-juniper woodlands. p. 39-51. In: G.J. Gottfried, J.D. Shaw, P.L Ford. Ecology, management, and restoration of piñon-juniper and ponderosa pine ecosystems: combined proceedings of the 2005 St. George, UT and 2006 Albuquerque, NM. Proceedings RMRS-P-51. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 218 p.

Presentations

Clifford, M.J. 2014. Rapid climate-induced tree die-off: patterns, mechanisms, and ecosystem response. Desert Research Institute. Las Vegas & Reno, NV. *Invited talk*

Redmond, M.D., N.S. Cobb, **M.J. Clifford**, and N.N. Barger. 2014. Future woodland composition in a changing climate: Abiotic and biotic controls on tree regeneration. 99th Ecological Society of America. Sacramento, CA. Oral

Gallego-Sala, A., S. Brewer, D. Charman, A. Blundell, R.K. Booth, **M.J. Clifford**, P. Friedlingstein, M. Garneau, V. Hohl, A. Lamarre, M. Lamentowicz, G. Magnan, D. Mauquoy, G.T. Swindles, S. van Bellen. 2013. Summer moisture balance from peatland water table reconstructions for the last 1100 years from North America and Europe. American Geophysical Union. San Francisco, CA. Poster

Clifford, M.J., K.A. LeBoeuf, and R.K. Booth. 2013. Abrupt change of late-Holocene forests in northeastern USA driven by drought and fire. 125th Geologic Society of America. Denver, CO. Oral

Clifford, M.J., K.A. LeBoeuf, and R.K. Booth. 2013. Drought and fire drove rapid changes in forest community composition in the northeastern United States. 98th Ecological Society of America. Minneapolis, MN. Oral

Clifford, M.J. and R.K. Booth. 2012. Late Holocene drought variability and wildfire occurrence in Maine. 97th Ecological Society of America, Portland, OR. Poster

Booth, R.K., A.W. Ireland, and **M.J. Clifford**. 2012. Forest and wetland response to Holocene moisture variability in eastern North America. 22nd American Quaternary Association Meeting. Duluth, MN. Invited talk

Clifford, M.J. and R.K. Booth. 2011. A stacked record of late-Holocene moisture variability from three raised bogs in Maine. American Geophysical Union. San Francisco, CA. Poster

Clifford, M.J. and R.K. Booth. 2010. Evidence for Medieval droughts in Maine and potential linkages to the coupled ocean-atmosphere system. American Geophysical Union. San Francisco, CA. Poster

Clifford, M.J., R.K. Booth*, J. Nichols. 2010. Multiproxy records of late Holocene climate variability from two raised bogs in Maine. 21st American Quaternary Association Meeting, Laramie, WY. (*presenter) Poster

Clifford, M.J., N.S. Cobb, and M. Buenemann. 2009. Spatiotemporal dynamics of a pinyon-juniper woodland: Proliferation, drought, and die-off. 24th US-International Association for Landscape Ecology Annual Meeting. Snowbird, UT. Oral

Clifford, M.J., N.S. Cobb, and P.L. Ford. 2008. A century of spatiotemporal dynamics of pinyon-juniper woodlands: Invasion, drought, and die-off. Southwest Regional Meeting of American Society of Photogrammetry and Remote Sensing at 52nd Arizona-Nevada Academy of Science. Phoenix, AZ. Oral

Cobb, N., K. Ironside, J.D. Shaw, C.D. Allen, D.D. Breshears, and **M. Clifford**. 2008. Tree mortality in response to global-change-type drought in the western US,

North America. International Symposium on Global Mountain Biodiversity. June 5-7, 2008, China Medical. Oral

Clifford, M.J., N.S. Cobb, and P.L. Ford. 2007. Patterns of drought induced tree mortality in pinyon-juniper woodlands. 9th Biennial Conference of Research on the Colorado Plateau. Flagstaff, AZ. Oral

Vespi, J.A., **M.J. Clifford**, and N.S. Cobb. 2007. Vegetation characteristics under three tree types within pinyon-juniper woodlands affected by drought related mortality. 9th Biennial Conference of Research on the Colorado Plateau. Flagstaff, AZ. Oral

Delph, R.J., **M.J. Clifford**, N.S. Cobb, and P. Ford. 2007. Impact of pinyon mortality on ground dwelling arthropods. 9th Biennial Conference of Research on the Colorado Plateau. Flagstaff, AZ. Oral

Cobb, N., K. Ironside, J.D. Shaw, K. Ogle, C.D. Allen, D.D. Breshears, and **M. Clifford**. 2007. Dieback of forests and woodlands across elevation gradients in response to global-change type drought in the southwestern, US, North America. Ecological Society of America/Society for Ecological Restoration Joint Meeting. San Jose, CA. Oral

Clifford, M., N. Cobb*, M. Rocca, R. Delph, and P. Ford. 2007. Drought impacts on southwestern pinyon-juniper woodlands. Ecology and Management of Pinyon-Juniper Ecosystems Symposium. Albuquerque, NM. (*presenter) Oral

Rocca, M.E., K. Ironside, **M. Clifford**, and N. Cobb. 2006. Impacts of drought and bark beetle-induced pine mortality on fire regimes in pinyon-juniper woodlands. 3rd International Fire Ecology and Management Congress. San Diego, CA. Poster

Clifford, M., N. Cobb, R. Delph, M. Rocca, and P. Ford. 2006. Stand characteristics of pinyon-juniper woodlands after a major drought event. 33rd Natural Areas Conference. Flagstaff, AZ. Oral

Delph, R., **M. Clifford**, N. Cobb, and P. Ford. 2006. Impact of drought and bark beetle outbreak on ground-dwelling arthropod dynamics in the pinyon-juniper woodlands in the Middle Rio Grande Basin. 33rd Natural Areas Conference. Flagstaff, AZ. Oral

Grants & Funding

2015 Clifford (PI) with Co-PIs J. Leyba & N.S. Cobb. Climate-induced patterns of juniper die-off: Response of fuels, understory plants, and invasive species to juniper die-off in Kasha-Katuwe Tent Rocks National Monument. USDI-Bureau of Land Management $23,000

2014 Co-PI with N.S. Cobb & P.L. Ford. Changing fuel loads from tree mortality on the Colorado Plateau through the southern Great Plains in response to drought and potential for Southwestern woodland tree species to alter future regional fuel loads. USDA-United States Forest Service $22,440

2013 Travel Grant, Earth and Environmental Science Dept., Lehigh University $400

2013 Travel Grant, Graduate Student Senate, Lehigh University $150

2013 Travel Grant, Geological Society of America $100

2013 College of Arts and Sciences Summer Research Fellowship, Lehigh University (2 month stipend)
2013 Travel Grant, Earth and Environmental Science Dept., Lehigh University $500
2012 Graduate Student Research Award, Earth and Environmental Science Dept., Lehigh University $750
2011 Travel Grant, Earth and Environmental Science Dept., Lehigh University $500
2009 US-International Association for Landscape Ecology Student Travel Award $500
2008 Co-PI (Co-PI: N.S. Cobb). Mapping of Lehmann Lovegrass and Agave Distributions at Fort Huachuca. Department of Defense $10,000
2006-2008 Co-PI (PI: N.S. Cobb). Impact of a Mega-Drought & Bark Beetle Outbreak on Piñon-Juniper Woodland Ecosystems in the Middle Rio Grande Basin. USDA United States Forest Service $108,000
2004 Albion Basin Eco-Geographic Study. Westminster College Undergraduate Research Grant $2,500

Services, Collaborations, Organizations, and Awards

Proposal reviewer:
National Science Foundation, Geography and Spatial Sciences Program (2014)
Northern Illinois University Opportunity Grants (2014)
Manuscript reviewer: *Global Ecology and Biogeography, New Phytologist*

2013 Graduate student representative to the Faculty, Earth and Environmental Science Department, Lehigh University
2010-2012 Committee and Chair, Graduate Student Travel Awards Committee, Earth and Environmental Science Department, Lehigh University
2007-2010 Geospatial Research And Information Laboratory (GRAIL)
2005-2010 Drought Impacts on Regional Ecosystem Network (DIREnet)
2007-2009 Vice-president NAU chapter of American Society for Photogrammetry and Remote Sensing (ASPRS)
2005 Outstanding Graduating Student in Biology, Westminster College